

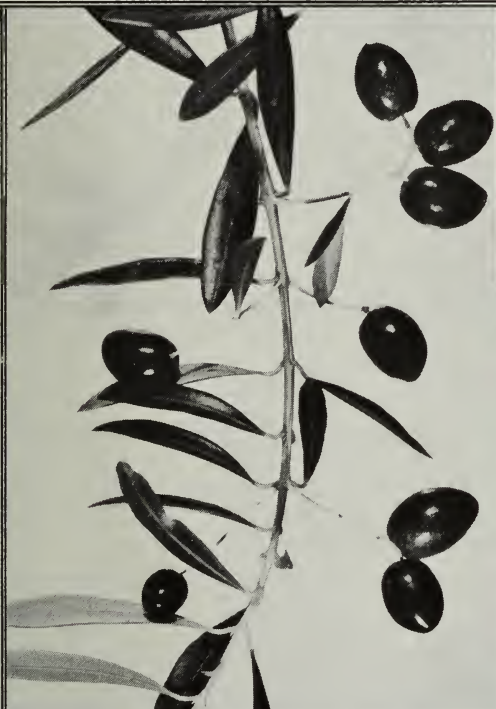


Division of Agricultural Sciences

UNIVERSITY OF CALIFORNIA

STACKS

# OLIVE POLLINATION IN CALIFORNIA



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EXPERIMENT STATION

BULLETIN 869

**T**his publication presents the results of an extensive study of the pollination status of the five main olive cultivars grown in California. It provides technical information for olive growers, horticulturists, plant science students, and research scientists.

Experiments conducted in University orchards, greenhouses, and laboratories, and in commercial orchards indicated that in most years cross-pollination results in larger and more uniform olive crops than does self-pollination. Studies of wind dissemination of olive pollen indicated the distances that wind may be expected to carry olive pollen for effective cross-pollination, and resulted in recommendations for interplanting cultivars for cross-pollination by wind.

A review of pertinent literature on olive pollination and a summary and recommendations are also presented.

Data and discussion include:

- flower structure, initiation, and fruit set
- effect of winter chilling on flower formation
- coincidence of bloom among olive cultivars
- collection of pollen, pollen viability, and dissemination of pollen by wind and bees
- controlled self- versus cross-pollination experiments conducted in orchards and greenhouses
- greenhouse and laboratory experiments regarding effect of temperature on pollen-tube growth and fruit set
- shotberry fruit production
- xenia in fruit development

**JANUARY 1975**

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# OLIVE POLLINATION IN CALIFORNIA<sup>1</sup>

California has over 42,000 acres of olives, with about 28,000 in bearing. Manzanillo, Sevillano, Mission, Ascolano, and Barouni are the principal cultivars, constituting approximately 44, 30, 21, 3, and 1 per cent, respectively, of the bearing acres.<sup>2</sup> Growers in each district tend to specialize in the production of one cultivar, but often an orchard contains more than one cultivar and several may be found in any one district.

Numerous satisfactorily yielding orchards are planted to a single cultivar.

On the other hand, some growers feel that cross-pollination increases yields and they point to some high-producing orchards with interplanted cultivars. Also, some isolated orchards planted solidly to one cultivar are less consistent in production than are comparable orchards with interplanted cultivars. Because of the lack of information on pollination requirements of olives in California and the potential benefits in providing proper pollination, the experiments reported herein were conducted to develop such information.

## REVIEW OF THE LITERATURE

**California.** Mills (1895) bagged flowering branches of olives in the Chino Valley (southern California) and concluded that most cultivars bear better when two or more are interplanted. Condit (1947), however, stated, "The consensus of opinion in California is that none of the olive varieties grown here requires cross-pollination and that interplanting of varieties is not necessary in order to insure greater fruitfulness." Griggs (1953) reported that commercial olive cultivars in California vary from year to year in their ability to set fruit after self-pollination and in certain years, therefore, it would pay to have pollenizers available. Bradley *et al.* (1961, 1963) studied pollen tube growth and fruit set after self- and cross-pollinations of Ascolano, Manzanillo, and Sevillano olive cultivars under warm and cool greenhouse conditions. They concluded that (a) pollen-tube growth was faster, (b) percentages of embryo sacs penetrated by pollen tubes were high-

er, and (c) fruit sets were higher in cross- than in self-pollinations. In general, pollen tubes grew faster in a warm than in a cool greenhouse.

**Italy.** Morettini and his co-workers (Morettini and Valleggi, 1940; Morettini and Benedetti, 1942; Morettini, 1950) reported that most of the olive cultivars grown in Toscana, Umbria, Roma, Lazio, and Pesciatino are self-incompatible. Gentile (1951) found that of the six most important cultivars grown in Pescara, four (Dritta, Castiglione, Olivoce, Indosso) were self-sterile and two (Carbonella, Police) were partly self-fertile. Fruit set of Carbonella and Police was greatly increased by cross-pollination.

**Portugal.** de Almeida (1940) believed the Portuguese olive cultivars to be self-fertile and stated that in Estremadura there are hundreds of hectares of high-yielding orchards planted solidly to Galega. He added that in Alentejo

<sup>1</sup> Submitted for publication April 12, 1974.

<sup>2</sup> The term "cultivar" (a contraction of "cultivated variety") is used in modern horticultural terminology in place of the less precise term, "variety."

there are high yields from large areas planted solidly to either Cordovil or Corrasguenba.

**Argentina.** Molinari and Nicolea (1947) described 16 olive cultivars including Ascolano, Manzanillo, and Sevillano, grown in Argentina. Only one, the Arauco, was considered self-sterile, but they recommended the Arbequina and Manzanillo as pollenizers for Arauco and stated that every other tree in every other row should be a pollenizer. Gerarduzzi (1957) concluded that most of their cultivars, including Manzanillo and Mission, were self-fruitful whereas Ascolano, Arauco, and Empeltre were partly self-fruitful, and Morinello was self-sterile. Wouters (1957) considered Ascolano, Manzanillo, Arauco, and Empeltre to be self-

incompatible. Vidal (1969) found that cross-pollination generally increased fruit set of Arauco, Frantoio, Leccino, Manzanillo, and Murtinha. Self-pollinated Manzanillo flowers gave 9.5 per cent fruit set; while those cross-pollinated with Arauco, Ascolano, Frantoio, Leccino, or Murtinha pollen gave, respectively, 10.5, 12.8, 17.2, 21.2, and 11.3 per cent set.

**Algeria.** From a study of eight cultivars (Chemlali, Sigoise, Limli, Bouchouk, Azeradj, Hamra, Rougette, and Picholine) in the Kabylia region, Chaux (1959) reported that most were either self-sterile or so weakly self-fertile that cross-pollination is necessary. Two, Chemlali and Hamra, were considered self-sterile because of anther abortion.

## FLOWERING AND FRUIT SET IN OLIVES

### Flower structure, initiation, and fruit set

Olive flowers are borne on inflorescences termed panicles (figs. 1, 2). The panicles of Barouni, Manzanillo, Mission, and Sevillano carry an average of from 12 to 18 flowers while those of Ascolano carry an average of about 20 flowers (table 1).

Individual flowers may be either perfect or imperfect. Perfect flowers normally consist of a small calyx, four petals, two stamens with large, pollen-bearing anthers, and a plump, green pistil with a short, thick style and a large stigma (figs. 3, 4; (King, 1938). Varying proportions of Sevillano flowers contain five petals, but flowers with six, seven, or eight petals may be found. Table 2 shows the average sizes of the different flower parts of five olive cultivars. Imperfect flowers are

Fig. 1. Manzanillo olive shoot with inflorescences.





Fig. 2. Inflorescences—Sevillano olive.

Fig. 3. Olive flower types. **Upper row:** perfect flowers, Ascolano; **Lower row:** staminate flowers, with pistils either lacking or rudimentary, Mission.





Fig. 4. Olive flower types, longitudinal sections. **Upper row:** perfect flowers, Ascolano; **Lower row:** staminate flowers, with pistils either lacking or rudimentary, Mission.

usually staminate, with the pistil either lacking or rudimentary (figs. 3, 4). Flowers with abortive anthers also occur and are fairly common in Sevil-

TABLE 1  
FRUIT SET, BASED UPON NUMBER OF INFLORESCENCES, FLOWERS, OR PERFECT FLOWERS, RESULTING FROM NATURAL POLLINATION OF INTERPLANTED OLIVE CULTIVARS AT WINTERS, 1951, 1952

Cultivar	Year	Number of inflores- cences	Number of flowers	Number of flowers per inflores- cence	Number of perfect flowers	Per cent perfect flowers	Mean number of fruits set per 100		
							Inflores- cences	Flowers	Perfect flowers
Ascolano . . . . .	1951	507	9,937	19.6	932	9.38	22.98	1.23	12.14
Ascolano . . . . .	1952	573	12,320	21.5	541	4.39	9.95	0.46	10.54
Barouni . . . . .	1951	769	13,842	18.0	2,925	21.13	9.10	0.50	2.43
Barouni . . . . .	1952	598	7,654	12.8	770	10.06	7.19	0.56	5.58
Manzanillo . . . . .	1951	337	4,819	14.3	2,219	46.05	22.55	1.58	3.42
Manzanillo . . . . .	1952	646	10,077	15.6	1,731	17.18	29.10	1.86	10.86
Mission . . . . .	1951	900	13,500	15.0	2,371	17.56	12.22	0.81	4.64
Mission . . . . .	1952	1,508	18,850	12.5	7,393	39.22	34.15	2.73	6.97
Sevillano . . . . .	1951	546	9,446	17.3	2,153	22.79	9.34	0.54	2.37
Sevillano . . . . .	1952	728	11,502	15.8	1,661	14.44	11.68	0.74	5.12

TABLE 2  
AVERAGE SIZE OF OLIVE FLOWER PARTS AT WINTERS, 1963\*

Cultivar	Diameter of flower (tip of one petal to tip of opposite petal)	Length of pistil	Length of ovary	Diameter of ovary	Length of stigma	Width of stigma	Thick-ness of stigma	Length of style	Length of anther	Width of anther	Thick-ness of anther	Length of filament
Ascolano. . . . .	8.17	3.80	1.72	1.47	1.30	0.77	0.77	0.78	3.03	2.28	1.15	1.12
Barouni. . . . .	7.66	2.90	1.57	1.62	0.95	0.76	0.52	0.38	3.25	2.25	1.50	1.00
Manzanillo . . .	7.20	3.04	1.47	1.36	1.20	0.82	0.58	0.37	2.65	2.50	1.10	0.60
Mission. . . . .	7.52	2.99	1.27	1.06	1.24	0.67	0.48	0.48	2.84	2.13	1.32	0.73
Sevillano. . . . .	8.37	3.65	2.41	2.42	1.10	1.03	0.75	0.14	2.68	2.24	1.46	1.52

\*Sizes given in millimeters.

lano. Figure 5 shows a longitudinal section of the pistil of a perfect flower with the parts indicated.

The percentage of perfect flowers is generally small but can vary widely (table 2). In some years, a tree may not develop enough perfect flowers to give a satisfactory crop even though it has produced a heavy bloom because of most of the flowers being staminate. Hartmann (1950) has shown that girdling such trees during December, January, and February may increase yields by increasing the percentage of perfect flowers. The trees must be fairly vigorous, however, for the practice to be effective. The relative proportion of perfect and staminate flowers varies greatly among inflorescences on the

same branch, as well as among branches, trees, cultivars, and seasons (Brooks, 1948; Hartmann, 1950). Usually, more of the perfect flowers are borne at the apical portion of an inflorescence than at the base. Individual flowers making up the inflorescence are often borne in groups of three, and the center one is most likely to be perfect. Perfect flowers reach anthesis (time of opening) before staminate ones on the same inflorescence (Brooks, 1948).

Olive trees usually bloom profusely and adequate commercial crops may be obtained even when only about 1 per cent of the total number of flowers set fruit (Hartmann, 1950). Pollen is produced in great abundance. The anthers of most perfect flowers are close enough to the stigma so that, at dehiscence, pollen falls or is thrown upon the stigma and self-pollination is accomplished. In some flowers, however, the filaments are flattened so that the anthers are spread away from the stigma, and in these flowers dehiscence does not ensure automatic self-pollination. Among cultivars grown in California, flowers with spreading anthers are the most prevalent in Ascolano. Flowers

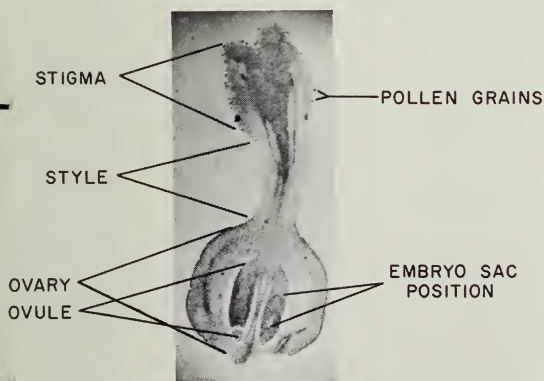


Fig. 5. Longitudinal section of olive pistil (27 times actual size).

are also wind-pollinated by air currents that distribute the tiny, yellow pollen grains throughout the orchard. Honeybees often visit olive flowers to gather pollen, but experiments in Italy (Morettini, 1950) and California (page 16) have shown that bees are not essential for olive pollination.

### **Effect of winter chilling on flower formation**

The olive tree does not survive winter temperatures below about 10° F. (−12° C). It makes good vegetative growth in equatorial regions having relatively warm winters, but in general the trees are not fruitful at latitudes below 30 degrees in northern or southern hemispheres. By bringing olive trees into the greenhouse after different periods of exposure to outdoor winter temperatures at Davis, Hartmann (1953) showed that flowering and fruitfulness are directly proportional to the amount of winter chilling. The amount of chilling required for maximum flower production varies with the cultivar (Hartmann and Porlingis, 1957; Porlingis, 1972).

Fruitfulness in California's deciduous fruits is also correlated with the amount of winter chilling, but there is a fundamental difference between the situation existing in olives and that in deciduous fruits. In deciduous fruits, flower-bud formation occurs during the summer; subsequent low winter temperatures serve to overcome the "rest period" of these buds, allowing them to develop normally in early spring rather than abscise or fail to open. With olives, Hartmann (1951) found that in California the first microscopic evidence of flower formation did not appear until about March 15, after the usual winter-chilling period. Hackett and Hartmann (1967) concluded that winter chilling is responsible for the initiation of floral parts,

and that the shy-bearing characteristics of olives in certain subtropical areas of the world may be explained on the basis of insufficient winter chilling.

Brown *et al.* (1962) added that in Tehama County, California, where in most years January temperatures are cold enough to favor flower-bud initiation, the temperatures in February and early March are also critical in relation to the number of flowers formed and the ultimate yield. The lower the temperatures during this period the greater were the yields.

### **Coincidence of blooming period among cultivars**

For satisfactory cross-pollination, two cultivars must have overlapping bloom periods. Figure 6 shows variations in the range of bloom periods as well as the average time of bloom of principal California olive cultivars. The 1954 bloom periods show the typical blooming sequence in response to gradual warming and predominately favorable weather early in May. In 1955, cold weather delayed the time of bloom and then sudden warm weather caused the cultivars to bloom at about the same time. In 1954, Ascolano bloomed a little late for best cross-pollination with Barouni. This combination therefore probably should not be recommended unless a third cultivar is provided for a pollinizer. In most years, however, there is enough overlap in bloom for adequate cross-pollination among the various cultivars grown in California.

### **Fruit set**

Fruit-set data were collected in 1951 and 1952 in an olive planting of mixed cultivars at the University of California's Wolfskill Experimental Orchard at Winters in the southern Sacramento Valley. As shown in table 1, consider-

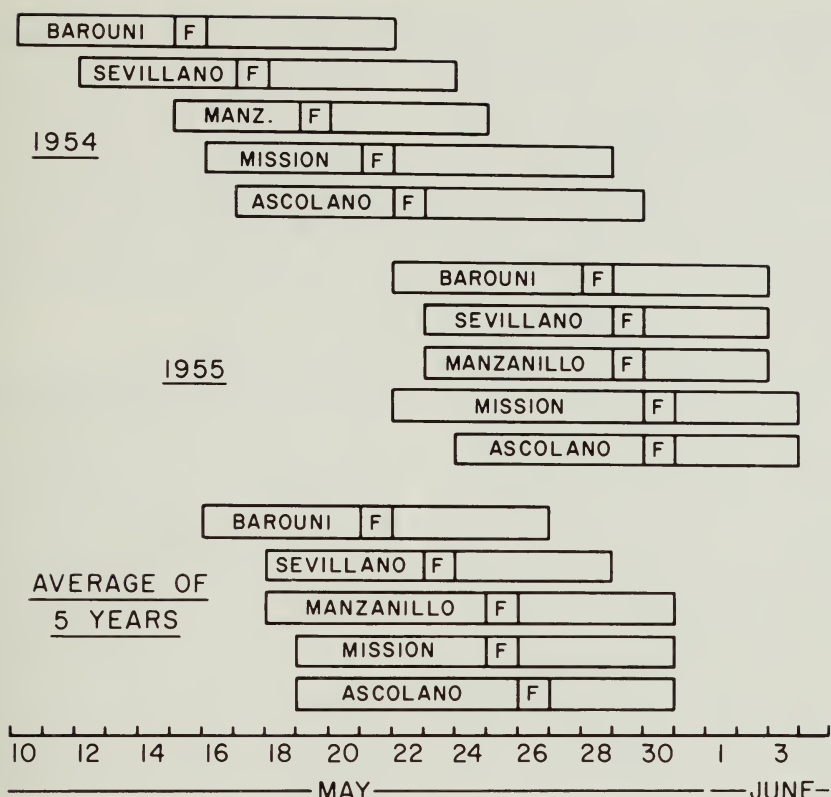


Fig. 6. Range of bloom periods for five olive cultivars at Davis. Bars indicate length of bloom from first conspicuous blossoms through full bloom (F) to last effective bloom.

able variability in fruit set can occur from year to year and among cultivars. Probably the best criterion for meas-

uring fruit set is the number of fruits developing from a given number of perfect flowers.

## OLIVE POLLEN

### Collection of pollen

With common deciduous fruit species, pollen for controlled artificial pollination is readily obtained by collecting flowers just before anthesis, separating the anthers in the laboratory, and then placing them on paper or cloth for dehiscence. This method is not satisfactory with the olive, however, because only very low percentages of the excised anthers dehiscence.

Pollen used in the experiments reported here was obtained in various ways. In one method, branches with unopened blossoms were taken from desired cultivars into the laboratory or greenhouse and held in buckets of water placed on window glass. As the anthers dehiscence some pollen dropped on the glass and periodically the flowering branches were removed and

thrashed against the glass; pollen and flower parts were then scraped from the glass with razor blades. Cheese cloth was used to sift out the flower parts and pollen was caught on smooth paper and transferred to vials. This method was unsatisfactory because many of the flowers failed to open and a large percentage of the anthers failed to dehisce.

However, an abundant supply of pollen could be obtained directly from blossoming trees by thrashing the ends of blossoming branches against panes of glass and using razor blades to scrape the pollen onto cheesecloth for sifting. To avoid contamination in this procedure, relatively isolated trees were used and the work was done early in the morning when there was little wind. When sections of olive trees were enclosed with nylon cages to prevent uncontrolled cross-pollination, this method yielded relatively large amounts of pollen from a few flowering branches in the cages—the abundance of pollen on the caged branches was due apparently to protection from the wind.

Olive trees growing in 5- and 10-gallon containers were used in some of the experiments reported here. Many of these trees produced heavy crops of flowers that could be forced into bloom ahead of orchard trees by bringing them into the greenhouse. Flowers on these trees dehisced normally and the pollen was collected from panes of window glass placed under them.

The most efficient method of gathering pollen was to enclose branches containing many unopened flowers in large, heavy paper bags. After most of the anthers had dehisced, the bags were removed and taken to the laboratory where the contents were emptied onto glass panes and the pollen recovered as previously described. If a

large portion of the flowers had not shed their pollen at the time a bag was removed, a new bag was placed over the branch for a later collection.

Pollen germination tests on agar-sugar-water media, as well as fruit sets effected by controlled artificial pollinations, revealed no consistent differences in pollen viability that could be attributed to the collection method.

### Pollen viability

Workers in Italy (Agati, 1951; Moretini, 1950) and Portugal (de Almeida, 1940) reported that olive pollen gave low germination percentages on artificial media. de Almeida (1940) found the best concentration of agar and sucrose to be 0.8 and 10 per cent, respectively, and the best temperature near 76.5° F (25° C). As changing the concentration within a small range did not give significant differences in germination, he concluded that low germinability was due to inherent factors. Moretini (1950) stated that the pollen of many fruit species germinates readily in aqueous solutions having 10 to 20 per cent sugar, but that olive pollen fails to germinate in such solutions.

Griggs *et al.* (1953) obtained 35.5 and 28.8 per cent germination of Manzanillo and Mission olive pollen, respectively, on 2 per cent agar and 15 per cent cane sugar after over 1 year storage at 0° F (−18°C). These percentages were approximately the same as those obtained when the pollen was first collected. Bradley *et al.* (1961) and Bradley and Griggs (1963) found no appreciable evidence of pollen sterility in studies of pollen tube growth after self- and cross-pollinations using Ascolano, Manzanillo, and Sevillano cultivars.

Germinability of the pollen used in the present study was determined by testing on plates of agar-sugar-water medium consisting of 2 per cent agar

TABLE 3  
EFFECT OF SUGAR CONCENTRATION ON GERMINATION OF OLIVE POLLEN ON  
AGAR-SUGAR-WATER MEDIUM\*

Variety of pollen	Date collected 1951	Germination per cent May 21, 1951†	
		On 12 per cent cane sugar	On 15 per cent cane sugar
Ascolano .....	May 17	30.7 a	23.0 a
Barouni .....	May 14	22.8 a	29.2 a
Manzanillo .....	May 15	22.3 a	23.8 a
Mission .....	May 15	28.2 a	21.4 a
Sevillano .....	May 15	30.8 a	27.6 a

\*All plates consisted of 2 per cent agar.

†Values are means of three or four replicates, each consisting of 100 to 200 pollen grains. Means for each variety followed by the same letter are not significantly different at the 5 per cent level.

and 15 per cent cane sugar. In one test, an agar-sugar medium consisting of 12 per cent cane sugar was compared with the standard 15 per cent cane sugar. There were no consistent differences in the germination percentages obtained with the two media (table 3).

A teasing needle was stirred into the vial of pollen to be tested. The pollen-coated needle was then removed, held over the agar-sugar medium, and gently tapped on the edge of the Petri dish to disperse the pollen onto the surface of the medium. The lid was then placed on the Petri dish and the pollen allowed to germinate at room temperature for 24 hours. A microscope was used to count the number of pollen grains which had formed relatively long pollen tubes as opposed to those which failed to germinate (or which produced only short tubes). Germination percentages were based on a total of 100 to 200 pollen grains per sample. Figures 7 and 8 show examples of germinating olive pollen. For each pollen variety, there was wide variation in the germination percentage among the dates of testing. Often, pollen stored for a year or more at 0° F (−18° C) gave higher germina-

tion percentages than that obtained with pollen taken from the same vial a day or two after collection.

Higher percentages of germination were obtained when fresh agar-sugar media were prepared for each testing, and when the Petri dishes containing the medium and the pollen were lidded to ensure high humidity. Atmospheric conditions had a noticeable effect on germinability even though the pollen was in a closed Petri dish. For example, high germination percentages were associated with southwest winds which increase humidity and often bring rain into the Sacramento Valley during winter and spring. On

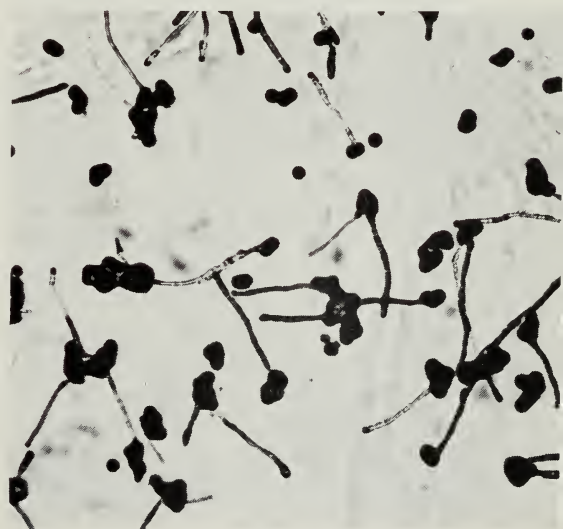


Fig. 7. Freshly-collected Mission olive pollen germinating on agar-sugar medium (130 times actual size).



Fig. 8. Mission olive pollen germinating on agar-sugar medium after 11 months storage at 0° F (−18° C); 200 times actual size.

the other hand, usually relatively low germination percentages occurred during periods when desiccative north winds were blowing strongly.

Table 4 shows germinability of olive pollen, which had been freshly collected, or collected after storage temperatures of 0° F (−18° C), 32° F (0° C), or 68° F (20° C). These germination percentages are about the same as those usually obtained with sweet cherry and Japanese and European plum pollen, and are high enough to indicate that all five California olive cultivars produce pollen of high viability. Germinability of the five varieties of pollen remained relatively high for more than 3 years when stored at 0° F (−18° C). Samples of the pollen also kept well when

stored at 32° F (0° C) for over 10 months. Pollen held at room temperature of approximately 75° F (24° C) from the time of collection from the tree in May showed little germination by July 14, but in other germinability tests (not shown in table 4) olive pollen maintained its original germination percentages for 2 or 3 weeks when stored at room temperature.

Because paper or cloth bags or nylon-covered cages were used to determine self-fruitfulness of olive cultivars and to eliminate uncontrolled cross-pollination, it was important to determine the effect of bagging and caging on pollen germinability. Pollen collected from flowers enclosed in paper bags gave about the same germination percentages on agar-sugar-water medium as did pollen from exposed flowers (table 5). Although the mean germination percentages of pollen from flowers enclosed in nylon-covered cages were somewhat lower than those from pollen collected from exposed flowers (table 6); except for Mission there were no consistent significant differences in the germinability of pollens taken from the two sources. It was concluded, therefore, that pollen that dehisced in the bags and cages was as viable or nearly as viable as pollen from exposed flowers, and that pollen collected from the bags and cages was satisfactory for use in pollination experiments.

### Dissemination of olive pollen

**Wind.** Olive trees usually bloom profusely and produce pollen in great abundance. When the anthers of a perfect flower dehisce, pollen is thrown upon the stigma and self-pollination occurs. Flowers are also wind-pollinated by air currents distributing pollen grains throughout the orchard.

Because wind is the primary agent for cross-pollinating olive flowers, the

TABLE 4  
EFFECT OF STORAGE TEMPERATURE ON GERMINATION OF OLIVE POLLEN\*

Cultivar	Date collected 1951	Storage temperature	Germination (per cent)					
			May 18-23, 1951	July 14, 1951	Sept. 12, 1951	April 7, 1952	May 23, 1953	October 12, 1954
Ascolano . . . . .	May 17	0° F (—18° C)	53.8	—	34.0	50.0	31.1	19.5
Barouni . . . . .	May 14	0° F (—18° C)	36.8	—	52.2	62.5	41.9	32.1
Manzanillo . . . . .	May 17	0° F (—18° C)	31.1	—	22.0	63.0	28.8	19.1
Mission . . . . .	May 15	0° F (—18° C)	69.9	—	46.6	65.9	34.4	28.3
Sevillano . . . . .	May 23	0° F (—18° C)	46.7	—	39.8	54.0	37.6	28.6
Ascolano . . . . .	May 17	32° F (0° C)	53.8	—	32.1	16.7	—	—
Barouni . . . . .	May 14	32° F (0° C)	36.8	—	35.8	19.7	—	—
Manzanillo . . . . .	May 17	32° F (0° C)	31.1	—	20.4	13.0	—	—
Mission . . . . .	May 15	32° F (0° C)	69.9	—	53.9	48.8	—	—
Sevillano . . . . .	May 23	32° F (0° C)	46.7	—	33.3	7.0	—	—
Ascolano . . . . .	May 17	Room temp. 75° F (24° C)	53.8	0.0	0.0	0.0	—	—
Barouni . . . . .	May 14	Room temp. 75° F (24° C)	36.8	2.0	0.5	0.0	—	—
Manzanillo . . . . .	May 17	Room temp. 75° F (24° C)	31.1	0.0	0.0	0.0	—	—
Mission . . . . .	May 15	Room temp. 75° F (24° C)	69.9	14.2	0.0	0.0	—	—
Sevillano . . . . .	May 23	Room temp. 75° F (24° C)	46.7	0.0	0.0	0.0	—	—

\*Pollen tested on an agar-sugar-water medium consisting of 2 per cent agar and 15 per cent cane sugar.

question arises as to how far the air currents may be expected to carry pollen in amounts necessary for cross-pollination. This information should help indicate the proportion and arrangement of pollinizer trees needed for adequate cross-pollination in an orchard planting. During the olive-blos-

soming period in Italy, Morettini (1940, 1950) placed glass panes coated with lanolin between two olive groves 2,300 feet apart and made counts of the pollen that settled on them after 3-day exposures. Plates located halfway between the two groves collected 0.61 pollen grains per square millimeter during

TABLE 5  
GERMINABILITY OF OLIVE POLLEN COLLECTED FROM BRANCHES ENCLOSED IN PAPER BAGS DURING BLOOM PERIOD COMPARED WITH GERMINABILITY OF POLLEN COLLECTED FROM EXPOSED BRANCHES;  
STORED FOR 12 MONTHS AT 0° F (—18° C)\*

Variety of pollen	Date collected 1950	Germination (per cent) May 15-17, 1951†	
		Pollen from bagged branches	Pollen from exposed branches
Ascolano . . . . .	May 15	20.0 a	17.9 a
Barouni . . . . .	May 15	25.1 a	29.7 a
Manzanillo . . . . .	May 15	29.3 a	25.9 a
Mission . . . . .	May 15	25.7 a	28.0 a
Sevillano . . . . .	May 15	22.4 a	24.3 a

\*Pollen tested on an agar-sugar-water medium consisting of 2 per cent agar and 15 per cent cane sugar.

†Values are means of two replicates, each consisting of 100 to 200 pollen grains. Means for each variety followed by the same letter are not significant at the 5 per cent level.

TABLE 6  
GERMINABILITY OF OLIVE POLLEN COLLECTED FROM TREES OF FIVE CULTIVARS  
IN NYLON-COVERED CAGES DURING BLOOM PERIOD COMPARED WITH  
GERMINABILITY OF POLLEN COLLECTED FROM EXPOSED TREES\*

Cultivar	Dates collected	Storage temperature	Dates tested	Germination (per cent)†	
				Pollen from caged trees	Pollen from exposed trees
Ascolano.....	May 11-17, '51	32° F	May 18-21, '51	31.2 b	53.8 a
Ascolano.....	May 11-17, '51	0° F	May 18-21, '51	29.5 a	40.6 a
Ascolano.....	May 11-17, '51	32° F	Sept. 12, '51	32.1 a	25.8 a
Ascolano.....	May 11-17, '51	0° F	Sept. 12, '51	22.9 a	35.6 a
Ascolano.....	May 11-17, '51	32° F	April 7, '52	16.7 a	11.3 a
Ascolano.....	May 11-17, '51	0° F	April 7, '52	21.4 a	29.8 a
			Means	25.6 a	32.8 a
Barouni.....	May 14-21, '51	32° F	May 18-21, '51	28.1 a	24.1 a
Barouni.....	May 14-21, '51	0° F	May 18-21, '51	23.4 a	28.4 a
Barouni.....	May 14-21, '51	32° F	Sept. 12, '51	33.7 a	35.8 a
Barouni.....	May 14-21, '51	0° F	Sept. 12, '51	52.2 a	42.7 a
Barouni.....	May 14-21, '51	32° F	April 7, '52	12.6 a	19.7 a
Barouni.....	May 14-21, '51	0° F	April 7, '52	45.7 a	50.3 a
			Means	32.6 a	33.5 a
Manzanillo.....	May 15-17, '51	32° F	May 18-21, '51	23.2 a	31.1 a
Manzanillo.....	May 15-17, '51	0° F	May 18-21, '51	27.5 a	33.8 a
Manzanillo.....	May 15-17, '51	32° F	Sept. 12, '51	12.7 a	20.4 a
Manzanillo.....	May 15-17, '51	0° F	Sept. 12, '51	21.9 a	36.6 a
Manzanillo.....	May 15-17, '51	32° F	April 7, '52	13.0 a	4.2 b
Manzanillo.....	May 15-17, '51	0° F	April 7, '52	25.5 a	35.5 a
			Means	20.6 a	26.9 a
Mission.....	May 14-21, '51	32° F	May 18-21, '51	20.3 b	39.3 a
Mission.....	May 14-21, '51	0° F	May 18-21, '51	37.1 a	43.7 a
Mission.....	May 14-21, '51	32° F	Sept. 12, '51	24.5 b	43.9 a
Mission.....	May 14-21, '51	0° F	Sept. 12, '51	36.2 a	41.9 a
Mission.....	May 14-21, '51	32° F	April 7, '52	10.8 b	38.8 a
Mission.....	May 14-21, '51	0° F	April 7, '52	45.8 a	48.0 a
			Means	29.1 b	42.6 a
Sevillano.....	May 23, '51	32° F	May 23, '51	41.1 a	32.5 a
Sevillano.....	May 23, '51	0° F	May 23, '51	41.1 a	32.5 a
Sevillano.....	May 23, '51	32° F	Sept. 12, '51	33.3 a	29.9 a
Sevillano.....	May 23, '51	0° F	Sept. 12, '51	38.8 a	32.9 a
Sevillano.....	May 23, '51	32° F	April 7, '52	2.0 a	7.0 a
Sevillano.....	May 23, '51	0° F	April 7, '52	42.8 a	36.2 a
			Means	33.2 a	28.5 a
			General means	28.2 a	32.9 a

\*Pollen tested on an agar-sugar-water medium consisting of 2 per cent agar and 15 per cent cane sugar.

†Values in the same row followed by the same letter are not significantly different at the 5 per cent level.

the early part of the blossoming period (June 15 through 18). Plates in the same location during full bloom (June 19 through 22), trapped 0.66 grains per square millimeter, and during the latter part of the blossoming period (June 24 through June 27), 0.20 grains per millimeter. In later studies Morettini and Pulselli (1953) found that under certain conditions the wind may

carry large quantities of olive pollen for about 10 miles. They state, however, that one cannot depend upon pollen being carried for such a distance, and they emphasize the importance of interplanting cultivars for cross-pollination. Morettini (1941) recommends planting one pollenizer tree for each 10 to 15 trees of the cultivar to be pollinated.

TABLE 7  
WIND DISSEMINATION OF OLIVE POLLEN AS SHOWN BY CONCENTRATION OF  
POLLEN GRAINS FOUND ON PETROLATUM-COATED PETRI DISHES PLACED ON  
THE LEEWARD SIDE OF BLOSSOMING TREES (DAVIS AND WINTERS)

Exposure time and distance from trees	Number of pollen grains per square millimeter		
	Ascolano	Mission	Varietal mixture
One hour of exposure at:			
10 feet . . . . .	0.53 (12-13)*	1.53 (2-4)	0.47 (12-13)
100 feet . . . . .	0.30	0.40	0.40
200 feet . . . . .	0.10	0.50	0.50
800 feet . . . . .	—	0.07	—
1000 feet . . . . .	0.00	—	0.00
Two hours of exposure at:			
10 feet . . . . .	0.27 (12-13)	2.33 (2-4)	—
100 feet . . . . .	0.33	0.20	—
200 feet . . . . .	0.27	0.07	—
800 feet . . . . .	—	0.03	—
1000 feet . . . . .	0.00	—	—
Four hours of exposure (3 hours for Mission) at:			
10 feet . . . . .	3.46 (2-5)	3.20 (6-8)	—
100 feet . . . . .	0.37	1.27	—
200 feet . . . . .	0.03	0.47	—
800 feet . . . . .	—	—	—
1000 feet . . . . .	0.03	—	—
Twenty-four hours of exposure at:			
10 feet . . . . .	—	9.73 (3-10)	—
100 feet . . . . .	—	2.13	—
200 feet . . . . .	—	1.13	—

\*All figures in parentheses are mph wind velocities.

To study wind dissemination of olive pollen in California, Petri dishes thinly coated with petrolatum were placed in small, open boxes about 4 inches above ground at various distances on the leeward side of blossoming trees. These were left exposed for periods varying from 1 hour to several

days, and at the end of the exposure lids were placed on the dishes, which were then taken to the laboratory for pollen-grain counts. In making such counts, the microscope was adjusted so that the field viewed through the eyepiece micrometer was limited to approximately 1 mm. The number of ol-

TABLE 8  
WIND DISSEMINATION OF SEVILLANO OLIVE POLLEN AS SHOWN BY  
CONCENTRATION OF POLLEN GRAINS ON PETROLATUM-COATED PETRI DISHES  
PLACED AT VARIOUS DISTANCES ON THE LEEWARD SIDE OF BLOSSOMING TREES  
(CORNING, MAY 18, 1951)

Distance from trees (miles)	Wind factors		Time exposed	Number of pollen grains per square millimeter
	Direction	Velocity (miles per hour)		
0.5 . . . . .	North	4 to 5	4 hours	0.79
1.6 . . . . .	North	4 to 5	4 hours	0.64
2.2* . . . . .	North	4 to 5	4 hours	0.18
3.2 . . . . .	North	4 to 5	4 hours	0.61

\*On top of hill.

ive pollen grains found in a square mm viewed was recorded for 20 different positions scattered over each Petri dish. These studies were conducted during 1951 through 1954, and the data shown in table 7 and figure 9 were selected as typical of the many similar trials. They show that the density of pollen grains greatly decreases as distance from the source is increased by an interval of 50 or 100 feet; density varied roughly in inverse proportion to the square of the distance from the source. Although pollen may be carried several hundred feet or even a few miles under certain conditions (table 8), it seems reasonable to conclude that if cross-pollination is to be effected, pollenizers must be interplanted in the orchard. The grower who plants solid blocks of one cultivar cannot expect air currents to supply enough pollen from a neighboring orchard to give the maximum benefit from cross-pollination.

To estimate the minimum number of pollenizer trees required and their distance from the principal cultivar, it is important to know more about the consistency with which pollen is liberated from the anthers and its germinability. The length of the blossoming period and the size and period of receptivity of the stigma of an individual flower are also important. There may be a variation of a week or more in the time of blossoming in different parts of a tree or branch. In the same inflorescence, the individual flowers may all open in 2 or 3 days or this period may be extended to as long as 10 or 12 days if there is a drop in temperature. In May of 1954 the stigmas of 12 Ascolano flowers were measured with a micrometer and it was concluded that the total surface of the stigma of this cultivar varies from approximately 2.5 to 3 square mm. From the reports of workers in

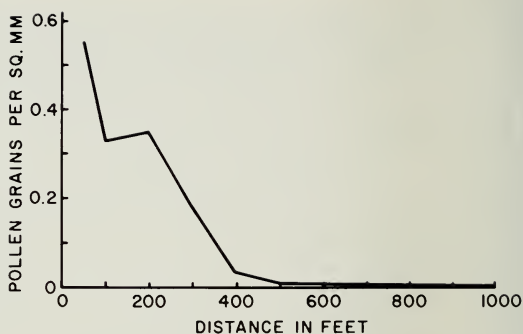


Fig. 9. Numbers of pollen grains per square millimeter found at increasing distances from the leeward side of a young olive orchard in Winters, California.

Italy, and from experience in these tests with bagging and cross-pollinating olive flowers, it seems likely that the receptivity of the stigma is maintained for a period of from 3 to 5 days after the flower opens.

In planting an olive orchard with two cultivars in equal numbers, it may be advisable, for convenience in harvesting, to plant four rows of one cultivar, then four of the other, then repeat. As olive trees are usually planted from 25 to 35 feet apart in squares, the above arrangement would ensure that most of the trees would not be over 70 feet from a pollenizing cultivar. This seems ideal for ensuring cross-pollination. If there is to be one principal cultivar, with trees of the pollenizing cultivar to be kept to a minimum, a planting arrangement using every third tree in every third row as a pollenizer should give satisfactory results.

**Bees.** Honeybees often visit olive blossoms to gather pollen. To determine the importance of bee visitation on fruit set, a branch on one tree of each cultivar used in the 1951 bagging experiments (p. 22) was enclosed throughout the blooming period with a 3-x 6-foot bag made of heavy mosquito-impervious netting. The net-

TABLE 9  
EFFECT OF BAGGING WITH MOSQUITO NETTING TO PREVENT BEE VISITATION ON  
FRUIT SET OF OLIVE CULTIVARS (DAVIS AND WINTERS, 1951)\*

Cultivar	Branches bagged with mosquito netting			Open pollination (cultivars interplanted)		
	Number of inflores- cences	Number of perfect flowers	Fruits set per 100 perfect flowers	Number of inflores- cences	Number of perfect flowers	Fruits set per 100 perfect flowers
Ascolano.....	527	124	47.6 a	507	932	12.1 b
Barouni.....	419	207	13.0 a	769	2,926	2.4 b
Manzanillo.....	425	714	36.7 a	337	2,219	3.4 b
Mission.....	1,292	1,831	28.1 a	900	2,371	4.6 b
Sevillano.....	460	1,382	7.0 a	546	2,153	2.4 b

\*For each cultivar, values for fruit set followed by different letters are significantly different at the 1 per cent level.

ting prevented bee visits but, presumably, allowed natural cross-pollination by wind-borne pollen. Table 9 shows the fruit sets on these branches and on the naturally pollinated controls. The high percentages of fruit set on branches protected by netting indicate that bee visits are not necessary for adequate olive crops. The heavy fruit sets experienced in this test may have been due to the wind protection afforded by the netting. In many years, gusty 15-20 mph north winds occur during olive blossoming in May in the Sacramento Valley. During these windy periods, olive branches are subjected to severe whipping. It was noted at the time the mosquito netting was removed that leaves and branches that had been enclosed were covered with pollen, whereas exposed branches were cleaned of pollen by the wind.

Although the 1951 experiments had shown that bee visitation is not essential for adequate fruit set in the olive, these studies were continued in 1952 to determine if frequent bee visits could increase fruit set.

During the first week in May (before flower opening) flowers were counted on four small Mission trees growing in 5-gallon containers and seven Oblonga trees in 1-gallon containers. One Mission and two Oblonga

trees were placed adjacent to each other within 15 feet of a row of honey-bee hives. These trees experienced constant bee visitation and, in addition, were subjected to air currents. Another Mission and two Oblonga trees were enclosed together nearby in a frame covered with mosquito-impervious netting. A second such cage enclosed two Mission trees, and a third enclosed three Oblonga trees. All the trees in the bee yard could have been cross-pollinated by pollen carried by the wind although there were no other olive trees within several hundred feet. From May 14 through 17, which included the full bloom period, a strong, desiccating, intermittent north wind prevailed, subjecting the olive branches to thrashing, and restraining bee activity. During calm periods, however, bees constantly visited the exposed olive flowers to gather pollen. On May 22 the trees were taken to the greenhouse where the number of perfect flowers on each tree were counted. They were kept in the greenhouse until late June when fruit-set counts were made.

To determine (as a comparison) the amount of fruit-set, resulting from self-pollination, three Mission and 18 Oblonga trees similar to those used in the bee yard were held separately in nylon cages (p. 34) in the greenhouse

TABLE 10  
EFFECT OF CROSS-POLLINATION BY HONEYBEE VISITATION  
ON FRUIT SET OF OLIVES (DAVIS, 1952)

Location and treatment	Cultivar	Number of trees	Number of inflorescences	Number of flowers	Number of perfect flowers	Number of fruits per 100 perfect flowers
In bee yard:						
1. Trees of one cultivar caged with mosquito netting	Mission	2	232	3,120	1,297	4.00*†
	Oblonga	3	85	1,458	865	9.36†
2. Trees of two cultivars caged together with mosquito netting	Mission and Oblonga	1	86	941	870	1.83
		2	32	711	384	8.59
3. Trees of two cultivars exposed together to honeybee visitation	Mission and Oblonga	1	144	1,618	296	7.43*‡
		2	45	768	218	18.81*†§
In greenhouse:						
4. Trees of one cultivar caged with nylon cloth to prevent cross-pollination	Mission	3	993	12,137	1,787	2.29*
	Oblonga	18	381	7,159	4,368	3.66

\*Significantly higher at the 1 per cent level than corresponding value under treatment 2.

†Significantly higher at the 1 per cent level than corresponding value under treatment 4.

‡Significantly higher at the 5 per cent level than corresponding value under treatment 1.

§Significantly higher at the 1 per cent level than corresponding value under treatment 1.

throughout the bloom period to prevent cross-pollination.

Table 10 summarizes the data from this study. Fruit sets on the trees exposed to cross-pollination by bees as well as by wind-blown pollen (treatment 3) were significantly higher than those obtained from trees held within the mosquito-netting compartments nearby (treatments 1 and 2), or in the nylon cloth compartments in the greenhouse (treatment 4). Evidently the honeybees effectively aided in cross-pollinating the olives and were responsible for the increased set. The relatively high fruit sets on the exposed trees were surprising since they

were subject to much more thrashing by strong winds than those in the nylon-covered compartments. The Oblonga trees held within the mosquito-netting compartments (treatments 1 and 2) must have received some cross-pollination by wind-blown pollen since they gave significantly heavier sets than the strictly self-pollinated Oblonga trees kept in the greenhouse (treatment 4). With Mission, the trees caged alone with mosquito netting (treatment 1) gave greater fruit set than did self-pollinated trees in the greenhouse (treatment 4), but those caged with Oblonga trees (treatment 2) did not.

## POLLINATION EXPERIMENTS

### 1950 experiments

Before the flowers opened, blossom counts were made on 15 to 25 selected branch units of mature Ascolano, Ba-

rouni, Manzanillo, Mission, and Sevilano trees at Winters and Davis. Two or three trees of each cultivar were

used. The branches were then enclosed in heavy 14-x 20-inch brown paper bags, or in 17-x 35-inch gabardine cloth bags, or were left as controls exposed to natural pollination. (Both types of bags were previously tested in the laboratory and found capable of excluding wind-borne olive pollen.)

The tops of the bags were wrapped and bound tightly to the branches with cloth and string to prevent entrance of unwanted pollen. Each paper bag enclosed about 1,350 flowers and each gabardine bag enclosed about 1,650. The control (unbagged) branches were assumed to be exposed to natural cross-pollination since the experimental orchards contained many trees of several cultivars. In the 1950 tests, the relative proportions of perfect and staminate flowers included in the experiments were not determined.

When the surrounding exposed flowers indicated that a good portion of the flowers in a bag had opened, a small hole was cut in the corner of the bag and a No. 4 capsule of the desired variety of pollen was puffed into it with a small hand aspirator (figs. 10 and 11). The stage of flower development in the bags could be determined by observation through the hole. A day or two later, depending on the weather and flower development, one or two additional capsules of pollen were puffed into the bag. After pollen was inserted, the holes in the cloth bags were closed with string and those in the paper bags were sealed with tape.

The cross-pollinations were made May 12 through May 22. Each treatment was replicated three times for each cultivar. Branches used to test the

Fig. 10. Equipment used for pollinating olives. Aspirators (right, top and bottom) used for pollinating olive flowers on shoots enclosed in bags. **Also shown:** glass rod (far left) used to apply pollen to individual flowers; a capsule of pollen (top) for loading into disassembled aspirator; and tweezers (center) for dipping capsule into vials of pollen (next to glass rod).

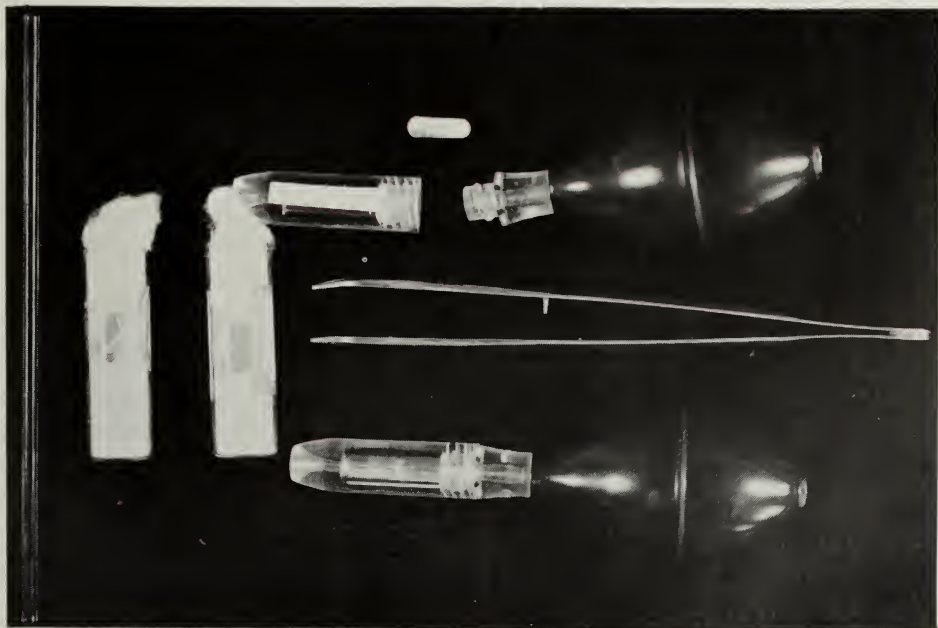




Fig. 11. Cross-pollinating olive flowers by inserting pollen with a hand aspirator into a cloth bag enclosing a flowering branch.

self-fruitfulness of the cultivars were left bagged throughout the blooming period. No pollen was inserted into them, but the branches in the bags were shaken to enhance self-pollination on the same days the cross-pollinations were made. Fruit set counts on the experimental branches were made on July 12 with the results shown in table 11.

The 1950 results showed the five principal olive cultivars grown in California to be practically self-incompatible and that cross-pollination would give significant increases in fruit set. Although the percentages of fruit set are relatively low, it should be remembered that they are based on the total number of flowers on the experimental branches rather than the number of perfect flowers (as used in later experiments). (Good commercial crops of olives may be obtained when only around 1 per cent of the total number of flowers set.)

Most of the branches bagged with gabardine and cross-pollinated gave significantly higher fruit sets than did the self-pollinated (bagged only) ones. A number of them also gave heavier sets than branches exposed to natural cross-pollination. Manzanillo showed the greatest response to cross-pollination, with Sevillano appearing to be the most effective pollenizer. Fruit set on the Sevillano trees was very low, and only the branches cross-pollinated with Mission pollen gave adequate set for commercial crops.

In general, fruit-set percentages for branches enclosed in paper bags were lower than for those in cloth bags. With Ascolano, Barouni, Manzanillo, and Mission, cross-pollination using paper bags usually gave significantly higher fruit sets than did self-pollination. However, only one combination of bagged and cross-pollinated treatments (Ascolano x Sevillano) with paper bags gave a significantly higher

TABLE 11  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON FRUIT SET IN  
SEVEN OLIVE CULTIVARS (DAVIS AND WINTERS, 1950)

Cultivar pollinated	Type of pollination	Pollenizer cultivar	Number of fruits set per 100 flowers*	
			In cloth bags	In paper bags
Ascolano . . . . .	Self only	Ascolano	0.0 c	0.1 c
Ascolano . . . . .	Self and cross	Barouni	0.8 a	0.3 b
Ascolano . . . . .	Self and cross	Manzanillo	—	0.1 c
Ascolano . . . . .	Self and cross	Mission	0.3 b	0.4 b
Ascolano . . . . .	Self and cross	Nevadillo	0.9 a	0.6 b
Ascolano . . . . .	Self and cross	Sevillano	1.0 a	1.2 a
Ascolano . . . . .	Open	Unknown	0.5 ab†	0.5 b†
Barouni . . . . .	Self only	Barouni	0.2 c	0.2 c
Barouni . . . . .	Self and cross	Ascolano	1.1 ab	0.6 b
Barouni . . . . .	Self and cross	Manzanillo	—	1.0 ab
Barouni . . . . .	Self and cross	Mission	0.9 b	1.0 ab
Barouni . . . . .	Self and cross	Nevadillo	0.4 c	0.6 b
Barouni . . . . .	Self and cross	Redding Picholine	—	1.4 a
Barouni . . . . .	Self and cross	Sevillano	1.7 a	0.2 c
Barouni . . . . .	Open	Unknown	0.6 b†	0.9 ab†
Manzanillo . . . . .	Self only	Manzanillo	0.0 d	0.0 c
Manzanillo . . . . .	Self and cross	Ascolano	2.3 b	1.3 a
Manzanillo . . . . .	Self and cross	Barouni	1.4 c	0.8 b
Manzanillo . . . . .	Self and cross	Mission	—	1.0 b
Manzanillo . . . . .	Self and cross	Nevadillo	—	0.7 b
Manzanillo . . . . .	Self and cross	Redding Picholine	2.4 b	0.6 b
Manzanillo . . . . .	Self and cross	Sevillano	4.4 a	1.1 ab
Manzanillo . . . . .	Open	Unknown	1.2 c†	1.1 ab†
Mission . . . . .	Self only	Mission	0.1 c	0.1 c
Mission . . . . .	Self and cross	Ascolano	0.9 b	0.1 c
Mission . . . . .	Self and cross	Barouni	1.3 b	1.2 a
Mission . . . . .	Self and cross	Manzanillo	—	0.7 ab
Mission . . . . .	Self and cross	Nevadillo	3.6 a	0.4 b
Mission . . . . .	Self and cross	Redding Picholine	—	0.8 ab
Mission . . . . .	Self and cross	Sevillano	1.5 b	0.5 b
Mission . . . . .	Open	Unknown	1.0 b†	1.0 a†
Sevillano . . . . .	Self only	Sevillano	0.0 c	0.1 b
Sevillano . . . . .	Self and cross	Ascolano	—	0.0 b
Sevillano . . . . .	Self and cross	Barouni	0.1 c	0.0 b
Sevillano . . . . .	Self and cross	Mission	1.4 a	0.1 b
Sevillano . . . . .	Self and cross	Nevadillo	0.0 c	0.0 b
Sevillano . . . . .	Open	Unknown	0.6 b†	0.6 a†

\*For each cultivar, means within each column followed by the same letter are not significantly different at the 5% level.

† Not bagged.

mean fruit set than did branches exposed to natural pollination. This indicated that the environment in the paper bags was not as favorable for fruit set as that provided by the cloth bags. Regardless of pollination treat-

ment, hardly any fruit was set on Sevillano branches enclosed in paper bags.

Fruit set resulting from self-pollination was determined on branches enclosed in bags throughout the bloom

period. If bagging reduced pollen viability, then nonviable pollen rather than self-incompatibility could have been responsible for low fruit sets on these branches. However, pollen germinability tests (tables 5, 6) indicated that the viability of pollen produced by flowers under bagged conditions was comparable to that from exposed flowers. Later studies showed also that branches bagged throughout the bloom period gave fruit sets comparable to the fruit sets obtained from branches that were bagged and then self-pollinated with pollen collected outside the bags and puffed into them by the same method used for cross-pollination.

1951 experiments

**Bagged branches.** Paper and cloth bags were used again in 1951 to determine fruit set resulting from self-pollination. The gabardine bags used in 1950 were replaced with larger (approximately 30- x 54-inch) double-thickness nylon bags, and larger (17- x 27-inch) heavy paper bags were used. Fruit set was calculated as the percentage of *perfect* flowers that set and developed normal fruit, rather than the percent-

age of the *total* number of flowers (perfect and staminate), as was done in 1950. The numbers of perfect flowers on the bagged branches were determined when bags were removed after petal fall.

Two or three bags of each type were placed on branches of each cultivar during the first 2 weeks in May (before the flowers opened) and were removed in June after petal fall. Similar branches exposed to natural pollination, including both self-pollination and cross-pollination by interplanted cultivars, was used as controls. Counts of final fruit set were made during the first week of July. Table 12 summarizes the results.

Fruit sets resulting from self-pollination of bagged flowers were surprisingly high in view of the previous year's results (and the results of other workers). Cloth bags again provided a more favorable environment for fruit set than did paper bags. With the exception of Sevillano, flowers of all cultivars enclosed in cloth bags during bloom also gave heavier fruit sets than did those of the open-pollinated controls, which had the benefit of self-pollination and natural cross-pollina-

TABLE 12  
EFFECT OF SELF-POLLINATION VERSUS NATURAL CROSS-POLLINATION ON THE  
FRUIT SET OF FIVE OLIVE CULTIVARS (DAVIS AND WINTERS, 1951)\*

Cultivar	Self-pollination						Open pollination, cultivars interplanted		
	In paper bags			In cloth bags					
	Number of inflores- cences	Number of perfect flowers	Fruits set per 100 perfect flowers	Number of inflores- cences	Number of perfect flowers	Fruits set per 100 perfect flowers	Number of inflores- cences	Number of perfect flowers	Fruits set per 100 perfect flowers
Ascolano . . . . .	974	2,019	2.2 c	402	361	20.0 a	507	932	12.1 b
Barouni . . . . .	707	2,761	2.6 b	676	1,373	7.9 a	769	2,926	2.4 b
Manzanillo . . . . .	314	309	1.0 c	232	285	17.9 a	337	2,219	3.4 b
Mission . . . . .	453	1,271	4.2 b	747	2,612	7.5 a	900	2,371	4.6 b
Sevillano . . . . .	186	877	0.4 b	791	3,049	0.8 b	546	2,153	2.4 a

\*For each cultivar, means for fruit set followed by the same letter are not significantly different at the 5 per cent level.

tion. Therefore, the bags must have afforded some protection against the strong, desiccative north winds.

These results indicate that under favorable conditions Ascolano, Barouni, Manzanillo, and Mission can give good commercial crops from self-pollination only. The ability of the flowers of these cultivars to set fruit from self-pollination and, consequently, the necessity or benefit of cross-pollination evidently varies greatly from year to year, possibly depending on environmental conditions.

**Enclosed caged trees.** Before bloom, sections of vigorous 8- to 10-year-old Ascolano, Barouni, Manzanillo, Mission, and Sevillano trees were enclosed in frames covered with double thicknesses of nylon or silk. These were approximately 8-feet square (fig. 12). The perfect flowers on branch units within the cages were given one of the following treatments: (1) self-pollina-

nation with pollen collected outside the cage; (2) natural self-pollination with pollen from within the cage (caged control); or (3) cross-pollination with pollen collected from caged portions of other cultivars. The pollen was applied to the stigmas by hand with a glass stirring rod (fig. 10). Eight to ten branches on the uncaged portion of each tree were used to determine the fruit set resulting from natural pollination, which included both self- and cross-pollination from trees of the interplanted cultivars.

The cages were removed in June after petal fall and final counts of fruit set were made in July. Fruits were collected from the experimental branches on November 30 through December 14 when most were changing from red to black. They were placed in cold storage and later subjected to various measurements for evidence of xenia—i.e., to determine whether or not cross-pollination results in larger fruits than self-pollination, and if the pollen parent differentially influences fruit and pit size.<sup>3</sup>

Fruit sets resulting from self-pollination of the caged control flowers were high in view of the previous year's results with bagged branches, and indicated that the degree of self-incompatibility of olive cultivars may vary widely from year to year (table 13). On the basis of the caged branches alone, only Mission benefited from cross-pollination. With the open or naturally pollinated flowers outside the cages, which were subject to both self- and cross-pollination, only Ascolano and Sevillano flowers gave significantly heavier sets than did caged controls. Viability of the pollen which

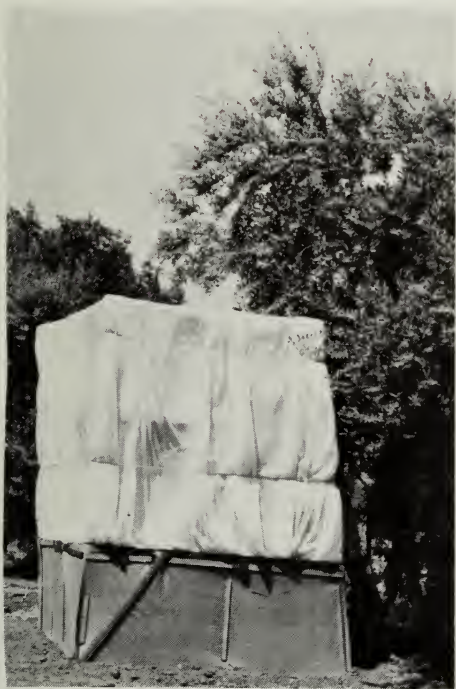


Fig. 12 Section of olive tree enclosed to prevent uncontrolled pollination. Frame covered with nylon cloth and burlap-coated paper.

<sup>3</sup> Xenia is the direct effect of one pollen variety versus another on fruit characteristics.

TABLE 13  
EFFECT OF DIFFERENT POLLINATION TREATMENTS ON FRUIT SET AND ON SIZE OF FRUIT, PIT, AND  
EMBRYO OF OLIVE CULTIVARS (DAVIS AND WINTERS, 1951)

Cultivar pollinated	Number of perfect flowers	Treatment		Cultivar of pollinizer	Mean number of fruits set per 100 flowers	Mean size of fruits, pits, and embryos at harvest, November 30, 1951 (shotberries not included) <sup>a</sup>				
		Caged or exposed*	Type of pollination			Fruit length (mm)	Fruit width (mm)	Pit length (mm)	Pit width (mm)	Embryo length (mm)
Ascolano.....	1,151	Caged	Self only (control)†	Ascolano	2.3	29.9ab	22.5b	19.1a	9.1a	12.7a
Ascolano.....	738	Caged	Self only (by hand)‡	Ascolano	1.9	28.0b	22.1b	18.9a	8.8a	12.9a
Ascolano.....	551	Caged	Self and cross	Barouni	0.8	—	—	—	—	—
Ascolano.....	733	Caged	Self and cross	Manzanillo	2.7	28.2b	22.0b	18.8a	9.4a	13.0a
Ascolano.....	741	Caged	Self and cross	Mission	2.4	29.0ab	21.5b	19.0a	8.8a	12.5a
Ascolano.....	452	Caged	Self and cross	Sevillano	1.3	30.3ab	23.0ab	18.6a	9.2a	12.9a
Ascolano.....	1,234	Exposed	Open	Unknown	8.3§	32.3a	24.3a	19.6a	9.3a	12.7a
Barouni.....	1,321	Caged	Self only (control)†	Barouni	2.6	29.5a	23.2a	19.5a	10.1a	12.9a
Barouni.....	621	Caged	Self only (by hand)‡	Barouni	0.5	28.0a	23.0a	19.0a	10.5a	13.0a
Barouni.....	649	Caged	Self and cross	Ascolano	0.0	—	—	—	—	—
Barouni.....	579	Caged	Self and cross	Manzanillo	0.2	—	—	—	—	—
Barouni.....	455	Caged	Self and cross	Mission	0.2	—	—	—	—	—
Barouni.....	478	Caged	Self and cross	Sevillano	0.2	28.0a	19.0a	19.5a	9.5a	12.6a
Barouni.....	2,400	Exposed	Open	Unknown	4.6	30.2a	23.1a	19.8a	10.0a	12.9a
Manzanillo.....	543	Caged	Self only (control)†	Manzanillo	6.8	23.3a	19.3ab	14.0a	8.1a	9.3a
Manzanillo.....	381	Caged	Self only (by hand)‡	Manzanillo	5.2	22.5ab	18.5b	13.8ab	8.1a	9.1a
Manzanillo.....	518	Caged	Self and cross	Ascolano	4.3	22.0b	18.8ab	13.6abc	8.0ab	8.9a
Manzanillo.....	339	Caged	Self and cross	Barouni	8.3	23.3ab	18.7b	13.6abc	8.0ab	9.2a
Manzanillo.....	485	Caged	Self and cross	Mission	5.4	23.6a	19.4a	14.0a	8.2a	9.2a
Manzanillo.....	726	Caged	Self and cross	Sevillano	7.0	22.2b	18.3b	13.1c	7.8b	9.0a
Manzanillo.....	2,219	Exposed	Open	Unknown	3.4	—	—	—	—	—
Mission.....	2,777	Caged	Self only (control)†	Mission	6.0	21.6b	15.2ab	16.1bc	7.5b	10.5ab
Mission.....	821	Caged	Self only (by hand)‡	Mission	7.9	20.4c	14.3c	15.3d	7.4bc	9.7c
Mission.....	1,379	Caged	Self and cross	Ascolano	11.3§	21.5b	15.5a	16.1bc	7.9a	10.2b
Mission.....	728	Caged	Self and cross	Barouni	13.5§	22.2a	15.2ab	17.1a	7.4bc	10.7a
Mission.....	1,115	Caged	Self and cross	Manzanillo	6.3	21.3b	15.6a	15.7cd	7.6b	9.7c
Mission.....	523	Caged	Self and cross	Sevillano	9.2§	21.7b	14.8bc	16.6ab	7.2c	10.5ab
Mission.....	2,371	Exposed	Open	Unknown	4.6	20.4c	15.3ab	15.2d	7.9a	10.3ab

Sevillano . . . . .	1,469	Caged	Self only (control)†	Sevillano	2.7	31.2a	25.1a	21.1a	10.6abc	13.1a
Sevillano . . . . .	525	Caged	Self only (by hand)‡	Sevillano	5.0	29.2b	21.7c	20.8a	10.1bc	13.2a
Sevillano . . . . .	716	Caged	Self and cross	Ascolano	2.8	30.4ab	23.6b	20.8a	10.6abc	13.4a
Sevillano . . . . .	452	Caged	Self and cross	Barouni	4.0	28.9b	23.1b	19.8a	9.8c	14.2a
Sevillano . . . . .	664	Caged	Self and cross	Manzanillo	3.0	30.3ab	24.2ab	20.6a	11.1ab	13.1a
Sevillano . . . . .	538	Caged	Self and cross	Mission	0.9	30.0ab	25.0a	20.6a	10.0bc	14.2a
Sevillano . . . . .	2,153	Exposed	Open	Unknown	2.4	31.8a	25.4a	21.7a	11.6a	13.5a

\*Portions of trees enclosed in nylon-covered cages during bloom to prevent uncontrolled pollination.

†Natural self-pollination of caged flowers.

‡Natural self-pollination of caged flowers plus self-pollination with pollen collected outside the cage.

§Significantly greater at the 1 per cent level than the mean for caged, self-pollinated control for the same cultivar.

||Significantly greater at the 5 per cent level than the mean for caged, self-pollinated control for the same cultivar.

¶For each cultivar, mean values in the same column followed by the same letter are not significantly different at the 5 per cent level.

dehiscid in cages apparently was equal to that of pollen collected from exposed flowers, since hand self-pollination with pollen collected outside the cages increased fruit set over caged controls in only two (Mission and Sevillano) of the five cultivars.

In general, the data indicate that xenia is not significant in determining the size of olive fruits. Although there were some differences in the mean size of fruits, pits, and embryos that developed under the different pollination treatments, these differences were not consistently related to self- versus cross-pollination or to the effectiveness of one pollenizer over another. Some differences in fruit size probably were due to the limited numbers of fruits developing under some treatments. Within the relatively low range of fruit sets obtained (0 to 11.3 per cent), however, there was no apparent correlation between fruit set and fruit size.

## 1952 experiments

**Enclosed caged trees.** During the first week in May—before blossom opening—vigorous, uniform 6-year-old olive trees at Winters were selected for the differential treatments. Flower clusters were counted on several branches of two Ascolano trees and on three trees each of Barouni, Columella, Manzanillo, Mission, and Sevillano. The trees were covered entirely with either two thicknesses of nylon to prevent all cross-pollination or with heavy mosquito-impervious netting to prevent visits from honeybees, or were left uncovered and used as naturally pollinated controls. Because trees of many other cultivars were interplanted in the orchard, conditions were ideal for cross-pollination. It was assumed that the mosquito-netting cages did



Fig. 13. Fruit development on typical shoots taken from self-pollinated nylon-caged trees (A) and from open-pollinated trees (B). Note more normal fruits and fewer shotberry fruits on the open-pollinated branches. Mission (upper left); Manzanillo (upper right); Sevillano (lower left); and Barouni (lower right).



Fig. 14. **Top:** types of olive fruits set on Sevillano olive trees about 3 weeks after full bloom. **Below:** development of similar fruits by late summer. **Left:** normal, seeded fruits. **Center and right:** parthenocarpic (shotberry) fruits without seeds. Center-type fruits often develop to about one-half full size and may be utilized for processing.

not prevent cross-pollination by wind-blown pollen, although flowers in these cages may have had less chance of being cross-pollinated than did those on the uncaged controls.

On May 26 and 27, after petal fall, the cages were removed and the perfect flowers on the experimental branches were counted. Counts of the final fruit set were made September 24. Figure 13 shows fruits from the nylon-caged self-pollinated branches and fruits from uncaged open-pollinated branches for four cultivars. Because large numbers of shotberry fruits developed on some branches, fruits were classified as either normal or shotberry (fig. 14). Shotberry olives (sometimes called "sports") are small, undesirable, presumably parthenocarpic fruit (Morettini, 1950; Pirota and De Pergola, 1915), most of

which persist until harvest. On November 12 the olives from the experimental branches were harvested and shotberry fruits were graded for size and examined for seed content. Tables 14 and 15 summarize the data.

The benefit of cross-pollination was indicated by the significantly higher fruit sets found on trees either enclosed with mosquito netting or exposed to natural pollination than were found on trees enclosed in the nylon-covered frames (table 14). However, the lower fruit sets on the trees in the nylon cages could have been due, at least in part, to a less favorable environment (possibly higher temperatures) rather than lack of cross-pollination. Columella was the exception: the trees in the nylon-covered cage had heavier fruit sets than did trees exposed to natural pollination.

TABLE 14  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON SET OF  
NORMAL AND SHOTBERRY FRUIT OF OLIVE CULTIVARS AT WINTERS, 1952, (TREES  
CAGED TO PREVENT BEE VISITATION OR NATURAL CROSS-POLLINATION)

Treatment	Cultivar	Number of inflores- cences	Number of perfect flowers	Mean number of normal fruits per 100 perfect flowers	Mean number of shotberry fruits per 100 perfect flowers
Trees caged with nylon	Ascolano	1,018	2,467	1.86	4.74*
	Barouni	1,098	3,729	1.10	0.00
	Columella	1,133	4,425	6.98*	1.38*
	Manzanillo	974	3,153	0.38	24.36*‡
	Mission	1,099	3,751	0.77	47.05*‡
	Sevillano	617	1,211	1.07	4.21*‡
Trees caged with mosquito netting	Ascolano	—	—	—	—
	Barouni	1,022	706	3.40†	0.14
	Columella	1,073	1,946	15.88*†	1.08
	Manzanillo	1,182	3,493	7.99†	11.36*
	Mission	1,115	4,084	8.69†	2.89
	Sevillano	552	560	3.04†	0.00
Trees naturally pollinated (cultivars interplanted)	Ascolano	1,151	3,769	3.45†	0.00
	Barouni	1,115	2,362	9.57†‡	0.00
	Columella	1,131	2,301	1.26	0.00
	Manzanillo	1,116	5,023	6.97†	3.34
	Mission	1,900	10,690	6.66†	3.52
	Sevillano	497	1,586	2.52†	0.32

\*Significantly higher at the 1% level than corresponding value for trees exposed to natural pollination.

†Significantly higher at the 1% level than corresponding value for trees caged with nylon.

‡Significantly higher at the 1% level than corresponding value for trees cages with mosquito netting.

TABLE 15  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON SEED  
DEVELOPMENT IN SHOTBERRY OLIVES AT WINTERS, 1952, (TREES CAGED DURING  
BLOOM TO PREVENT BEE VISITATION OR NATURAL CROSS-POLLINATION)

Approximate size of shotberry fruit									
Treatment	Cultivar	2/3 to 1/2 of normal		1/2 to 1/4 of normal		1/4 normal and less		Total number exam- ined	Per cent seedless
		Seeded	Seedless	Seeded	Seedless	Seeded	Seedless		
Trees caged with nylon	Ascolano	10	22	3	15	0	56	106	87.7
	Columella	0	17	0	55	0	12	84	100.0
	Manzanillo	0	0	0	3	0	93	96	100.0
	Mission	3	4	0	35	0	553	595	99.5
	Sevillano	0	6	0	12	0	24	42	100.0
Trees caged with mosquito netting	Barouni	0	0	1	0	0	0	1	0.0
	Columella	2	1	1	21	0	7	32	90.6
	Manzanillo	0	4	0	8	0	146	158	100.0
	Mission	0	0	6	7	0	29	42	85.7
	Sevillano	0	3	0	0	0	0	3	100.0
Trees naturally pollinated (cul- tivar interplanted)	Manzanillo	0	0	5	8	0	57	70	92.9
	Mission	7	0	5	21	0	200	233	94.8
	Sevillano	0	7	1	11	0	3	22	95.4

With the exception of Columella, trees enclosed in mosquito-netting-covered cages (tables 14) did not have the striking increases in set obtained the previous year (table 9) when individual branches were enclosed with the same material. The sets on these trees were high enough, however, to corroborate the conclusion that honeybees are not essential for commercial crops of olives.

Cross-pollination evidently reduced the production of shotberry fruit, as trees caged with nylon to prevent cross-pollination produced significantly more shotberries than did those enclosed with mosquito netting or exposed to natural pollination (table 14). Self-pollinated Manzanillo and Mission flowers produced relatively high percentages of shotberries. With Ascolano, Manzanillo, Mission, and Sevillano, high sets of normal fruit were accompanied by low production of shotberries and vice-versa.

Pollination treatment evidently had no effect on size or seed content of

shotberry olives (table 15). All examined shotberries contained an endocarp (pit). Pits of the smallest shotberries were only about 3 mm long, while normal pit-length ranged from an average of about 13 mm for Manzanillo to 22 mm for Sevillano. Pits of most shotberries were seedless and contained only the shriveled remains of the integuments (seed coats). A few of the larger fruits, thought to be shotberries contained embryos, but they were smaller than normal. For example, embryos of normal Manzanillo fruits were approximately 10 mm long as compared to the 7-mm length of the few embryos found in shotberry fruits of this cultivar. Any shotberry fruit containing an embryo, regardless of size, was tabulated as seeded. Of shotberries harvested from the five cultivars enclosed in nylon cages during bloom, 80 per cent were small (one-fourth normal size or less) and seedless, while 77 and 80 per cent, respectively, of those produced by the trees enclosed with mosquito netting or ex-

posed to natural pollination were small and seedless. Most of the shotberries in the larger size groups were also seedless.

**Bagged branches.** Other 6-year-old trees in the same block at the University of California Wolfskill Experimental Orchard at Winters were used to determine the effect of artificial cross-pollination on fruit set and size. Inflorescences were counted on six to eight branches on three trees of each cultivar. Then all branches, except those used as naturally pollinated controls, were bagged with double-thickness nylon cloth bags approximately 30-x 54-inches in size. Most of the pollen was collected from exposed branches of relatively isolated trees 3 or 4 days before it was used. To determine the effectiveness of stored versus freshly collected pollen, however, some of the branches were cross-pollinated with pollen collected the previous year and stored at 0° F (-18° C).

When most of the blossoms were open (May 18 through 22) capsules of pollen were puffed into each bag by inserting an aspiratory nozzle through a small hole in the corner of the bag (fig. 11). Each artificially pollinated branch received a total of two or three capsules of pollen at 2- or 3-day intervals. Fruit set resulting from self-pollination was determined in two ways: by bagged-only controls, and by collecting pollen from exposed branches of relatively isolated trees of the same cultivar and puffing it into the bags. A comparison of fruit sets resulting from the two types of self-pollination would indicate the relative viability of pollen produced in the bags and that produced by exposed flowers.

On May 27 through 29, after petal fall, the bags were removed and perfect flowers on all experimental branches were counted. Final fruit-set counts of both normal and shotberry

olives were taken from September 24 through October 6. Fruits on the experimental branches were harvested November 12, when most were changing from red to black, and placed in cold storage. Later, normal fruits were subjected to various measurements for evidence of xenia and shotberry fruits were graded for size and examined for seed content. Tables 16, 17, and 18 summarize the results.

Cross-pollination, by either artificial or natural means generally produced significantly higher fruit sets than did self-pollination (table 16). There was an indication of inter-incompatibility between Sevillano and Barouni and between Mission and Manzanillo because fruit sets resulting from cross-pollinations between these cultivars did not equal those from others.

These results gave further evidence that cross-pollination reduces the production of shotberries, as most of the cross-pollinated Manzanillo and Mission flowers produced significantly fewer shotberries than did the self-pollinated ones (table 16, fig. 13). The other cultivars produced few shotberries regardless of treatment. Although fruit sets resulting from reciprocal crosses between Manzanillo and Mission were relatively low, all the fruits were normal. However, self-pollinated branches of these cultivars produced relatively high percentages of shotberries. There was no indication that pollination treatment affected the size or seed content of shotberry olives (table 17). Most shotberry fruits were small and seedless.

Measurements of normal fruits (shotberry fruits excluded) and their pits (table 18) showed no clear-cut evidence of xenia among the olive cultivars. Size of fruits and pits resulting from self-pollination alone were not consistently different from those re-

TABLE 16  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON SET OF  
NORMAL AND SHOTBERRY FRUIT (WINTERS AND DAVIS, 1952)

Cultivar pollinated	Number of inflores- cences	Number of perfect flowers	Branch units bagged with nylon during bloom to prevent uncontrolled pollination					Open pollination (cultivar trees interplanted)	
			Pollen cultivar applied						Bagged only
			Ascolano	Barouni	Manzanillo	Mission	Sevillano		
Ascolano	1,183	1,030	Normal: Shotberry:	5.46 0.42	19.44*† 0.00	— —	1.32 0.00	21.09*† 0.00	10.54*§ 0.00
Barouni	2,138	3,990	Normal: Shotberry:	12.50*† 0.00	2.14 0.00	— —	7.94*† 0.00	3.51 0.00	5.58*† 0.00
Columella	1,997	7,687	Normal: Shotberry:	8.48‡ 1.20	24.54* 0.18‡	— —	6.92 0.76	23.59* 0.28‡	5.55 0.14
Manzanillo	2,009	5,803	Normal: Shotberry:	5.34*§ 0.21*†	21.95*† 0.00*†	1.16 31.79	3.38* 0.00*†	30.32*† 0.00*†	10.86*† 0.00*†
Mission	4,175	21,183	Normal: Shotberry:	7.04*† 7.72*	16.74*† 0.00*†	1.86 0.00*†	4.96 9.24*	13.80*† 1.26*†	6.97*† 8.20*
Sevillano	1,932	3,783	Normal: Shotberry:	10.81*† 0.00	2.92 0.00	— —	4.50†‡ 0.00	1.12 0.00	5.12†‡ 0.12

Normal fruit set:

\*Significantly greater at the 1% level than corresponding value for self-pollination on branches bagged only.

†Significantly greater at the 1% level than corresponding value for branches self-pollinated with pollen collected outside the bag.

‡Significantly greater at the 5% level than corresponding value for self-pollination on branches bagged only.

§Significantly greater at the 5% level than corresponding value for branches self-pollinated with pollen collected outside the bag.

Shotberry fruit set:

\*Significantly smaller at the 1% level than corresponding value for self-pollination on branches bagged only.

†Significantly smaller at the 1% level than corresponding value for branches self-pollinated with pollen collected outside the bag.

‡Significantly smaller at the 5% level than corresponding value for self-pollination on branches bagged only.

§Significantly smaller at the 5% level than corresponding value for branches self-pollinated with pollen collected outside the bag.

TABLE 17  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON  
SEED DEVELOPMENT OF SHOTBERRY OLIVES AT WINTERS AND DAVIS, 1952,  
(BRANCH UNITS BAGGED WITH NYLON DURING BLOOM  
TO PREVENT UNCONTROLLED POLLINATION)

Cultivar	Treatment	Approximate size of shotberry fruit						Total number exam- ined	Per cent seedless
		2/3 to 1/2 of normal		1/2 to 1/4 of normal		1/4 normal and less			
		Seeded	Seedless	Seeded	Seedless	Seeded	Seedless		
Columella . . . .	Bagged only	0	1	0	12	0	3	16	100.0
Columella . . . .	X Ascolano	0	0	0	8	0	2	10	100.0
Columella . . . .	X Barouni	0	0	0	1	0	1	2	100.0
Columella . . . .	X Mission	3	5	0	19	0	5	32	90.6
Columella . . . .	X Sevillano	0	0	3	4	0	1	8	62.5
Columella . . . .	Open pollination	0	0	0	3	0	1	4	100.0
Manzanillo . . . .	X Manzanillo	0	0	0	0	0	45	45	100.0
Manzanillo . . . .	Bagged only	0	0	0	2	0	53	55	100.0
Manzanillo . . . .	X Ascolano	0	0	0	0	0	2	2	100.0
Mission . . . . .	X Mission	0	0	0	3	0	84	87	100.0
Mission . . . . .	Bagged only	0	1	1	9	0	300	311	99.7
Mission . . . . .	X Ascolano	0	0	0	4	0	78	82	100.0
Mission . . . . .	X Sevillano	0	0	0	0	0	36	36	100.0
Mission . . . . .	Open pollination	0	0	2	9	0	287	298	99.3
Sevillano . . . . .	Open pollination	0	0	0	1	0	1	2	100.0

sulting from self- plus cross-pollination. Also, there were no consistent differences in fruit size that could be attributed to the use of one pollinizer or another. For each cultivar, size of fruits was remarkably uniform regardless of pollination treatment.

Pollen stored for a year at 0° F (−18° C) was nearly as effective in cross-pollination as freshly collected pollen (table 19). This supports the results of viability tests on agar-sugar medium (table 4) indicating that germinability of stored pollen was about the same as that of fresh pollen. Fresh Sevillano pollen gave significantly greater fruit sets than did stored Sevillano pollen, but stored Manzanillo pollen gave significantly heavier sets than did freshly collected pollen. Regardless of pollen age, most cross-pollinations gave heavier fruit sets than did those resulting from self-pollination on the bagged branches. The fact that Mission branches cross-pollinated with the previous year's Manzanillo pollen gave significantly heavier sets

than did self-pollinated branches is inconsistent with previous data (table 16) which indicated that these cultivars might be inter-incompatible.

**Greenhouse experiments.** Because of contradictory results regarding the degree of self-incompatibility and the effects of cross-pollination on fruit set, a greenhouse study was designed to eliminate the influence of strong winds and temperature extremes.

During the first week in May, before flower opening, flowers were counted on each of five Barouni and seven Mission trees growing in 5-gallon containers, and on 25 Manzanillo trees in 1-gallon containers. The Barouni and Mission trees were 5, and the Manzanillo 3 years old. The trees were then placed in 4-x 5-x 6-foot frames covered with double-thickness nylon cloth which had been set up in the greenhouse (fig. 15). The nylon covering prevented uncontrolled pollination. Three compartments enclosed trees of a single cultivar to prevent

TABLE 18  
EFFECT OF POLLEN PARENT ON THE SIZE OF FRUITS AND PITS OF OLIVE CULTIVARS  
AT HARVEST (WINTERS AND DAVIS, 1952)

Mean size of fruits and pits at harvest, November 12, 1952 (Shotberries not included) <sup>†</sup>							
Treatment		Pollenizer cultivar	Fruit length (mm)	Fruit width (mm)	Pit length (mm)	Pit width (mm)	
Bagged or exposed*	Type of pollination						
Ascolano . . . . .	Bagged	Self only (control)	27.7a	23.4a	16.8a	9.4a	
Ascolano . . . . .	Bagged	Self only (by hand) <sup>†</sup>	25.0b	21.1b	16.3a	8.6a	
Ascolano . . . . .	Bagged	Self and cross	27.5ab	23.0a	16.6a	9.3a	
Ascolano . . . . .	Bagged	Self and cross	28.0a	24.1a	16.4a	9.7a	
Ascolano . . . . .	Bagged	Self and cross	25.5b	20.8b	16.1a	8.7a	
Ascolano . . . . .	Exposed	Open	28.1a	23.7a	16.8a	9.3a	
Barouni . . . . .	Bagged	Self only (control)	26.4ab	22.0a	16.9a	10.0ab	
Barouni . . . . .	Bagged	Self only (by hand)	26.5ab	21.7ab	17.7a	9.5bc	
Barouni . . . . .	Bagged	Self and cross	26.4ab	20.9b	17.6a	9.2c	
Barouni . . . . .	Bagged	Self and cross	27.8a	23.1a	18.4a	10.5a	
Barouni . . . . .	Bagged	Self and cross	26.6ab	22.0a	17.3a	9.8b	
Barouni . . . . .	Exposed	Open	26.1b	20.6b	18.0a	9.8b	
Columella . . . . .	Bagged	Self only (control)	21.6b	17.8ab	14.2ab	7.8b	
Columella . . . . .	Bagged	Self and cross	21.4b	17.6b	14.2ab	8.0ab	
Columella . . . . .	Bagged	Self and cross	22.4a	18.2a	14.5ab	8.2a	
Columella . . . . .	Bagged	Self and cross	21.4b	17.6b	14.1b	8.0ab	
Columella . . . . .	Bagged	Self and cross	21.2b	17.4b	14.1b	7.8b	
Columella . . . . .	Exposed	Open	22.3a	18.3a	14.6a	8.2a	
Manzanillo . . . . .	Bagged	Self only (control)	23.9a	20.9a	13.9a	9.1a	
Manzanillo . . . . .	Bagged	Self only (by hand)	22.0bc	19.4cd	14.1a	8.8ab	
Manzanillo . . . . .	Bagged	Self and cross	22.6bc	20.1b	13.7a	8.8ab	
Manzanillo . . . . .	Bagged	Self and cross	22.3bc	19.4cd	13.1c	8.4c	
Manzanillo . . . . .	Bagged	Self and cross	22.3bc	19.4cd	12.9c	8.4c	
Manzanillo . . . . .	Bagged	Self and cross	21.9c	19.1d	13.3bc	8.1d	
Manzanillo . . . . .	Exposed	Open	22.9b	19.9bc	13.6ab	8.6b	
Mission . . . . .	Bagged	Self only (control)	19.9ab	15.0a	14.5a	7.7b	
Mission . . . . .	Bagged	Self only (by hand)	19.4bc	14.8a	14.4ab	7.9b	
Mission . . . . .	Bagged	Self and cross	19.6ab	15.5a	14.2abc	8.2a	
Mission . . . . .	Bagged	Self and cross	18.9c	14.6a	14.0bc	7.8b	
Mission . . . . .	Bagged	Self and cross	19.4bc	14.7a	14.3abc	7.8b	
Mission . . . . .	Bagged	Self and cross	19.0bc	14.6a	13.9c	7.8b	
Mission . . . . .	Exposed	Open	20.2a	16.0a	14.2abc	8.3a	

(continued next page)

TABLE 18  
EFFECT OF POLLEN PARENT ON THE SIZE OF FRUITS AND PITS OF OLIVE CULTIVARS  
AT HARVEST (WINTERS AND DAVIS, 1952)

Cultivar pollinated	Treatment		Mean size of fruits and pits at harvest, November 12, 1952 (Shotberries not included) <sup>‡</sup>				
	Bagged or exposed*	Type of pollination	Pollenizer cultivar	Fruit length (mm)	Fruit width (mm)	Pit length (mm)	Pit width (mm)
Sevillano .....	Bagged	Self only (control)	Sevillano	31.8a	26.9a	20.7a	11.7a
Sevillano .....	Bagged	Self only (by hand)	Sevillano	32.7a	25.5b	23.5a	10.8bc
Sevillano .....	Bagged	Self and cross	Ascolano	31.1a	25.2b	21.3a	10.7c
Sevillano .....	Bagged	Self and cross	Barouni	33.8a	27.1a	23.1a	11.4ab
Sevillano .....	Bagged	Self and cross	Mission	31.7a	25.6b	22.9a	11.1b
Sevillano .....	Exposed	Open	Unknown	32.2a	27.2a	21.3a	11.7a

\*Branch units bagged with nylon during bloom to prevent uncontrolled pollination.

†Self-pollination of bagged flowers plus self-pollination with pollen collected outside bag.

‡For each cultivar, mean values in the same column followed by the same letter are not significantly different at the 5 per cent level.

cross-pollination, and three compartments enclosed trees of two cultivars to permit controlled cross-pollination. The greenhouse temperatures ranged from about 60° F (15.6° C) at night to 90° F (32° C) during the day.

A 12-inch-blade electric fan was placed in each compartment, and throughout the bloom period (May 8 through 19) they were run at low speed for 20-minute periods twice daily to simulate wind dissemination of pollen. There was an overlap of several days in the bloom periods of the paired cultivars in the cages, which would favor cross-pollination.

On May 24, after petal fall, the trees were removed from the compartments and all perfect flowers were counted. The trees were left in the greenhouse and counts of fruit set were made in late June. Table 20 summarizes the results. The extreme variation in the numbers of perfect flowers produced among the cultivars emphasizes the difficulty of determining the pollina-

Fig. 15. Series of 4- × 5- × 6-foot nylon-covered compartments used in greenhouse olive pollination experiments.



TABLE 19  
EFFECT OF CROSS-POLLINATION WITH POLLEN STORED FOR 1 YEAR AT 0° F (−18° C)  
VERSUS FRESHLY COLLECTED POLLEN ON FRUIT SET OF OLIVES AT WINTERS, 1952  
(BRANCH UNITS BAGGED WITH NYLON DURING BLOOM TO PREVENT  
UNCONTROLLED POLLINATION)

Cultivar	Number of inflores- cences	Number of perfect flowers	Pollen cultivar	Mean number of fruits set per 100 perfect flowers		
				With pollen collected		Control (bagged only)
				1951	1952	
Ascolano . . . . .	341	196	Mission	5.50	1.32	0.00
Barouni . . . . .	712	1,729	Mission	7.14*	7.94*	2.17
Columello . . . . .	562	2,055	Mission	7.78	6.92	6.68
Columello . . . . .	573	2,135	Sevillano	12.74*	23.59*†	6.68
Mission. . . . .	942	4,451	Manzanillo	7.14*†	1.86	4.08
Mission. . . . .	1,087	6,565	Sevillano	9.96*	13.80*†	4.08
Sevillano . . . . .	688	828	Ascolano	13.33*	10.81*	1.56
Sevillano . . . . .	678	971	Mission	1.96	4.50‡	1.56

\*Significantly greater at the 1% level than corresponding value for self-pollination on branches bagged only.  
†Significantly greater at the 1% level than corresponding value for either fresh or one-year-old pollen.  
‡Significantly greater at the 5% level than corresponding value for self-pollination on branches bagged only.

tion status of the olive. The small, self-pollinated Manzanillo trees produced a total of only 33 perfect flowers. The fact that 54.5 per cent of these flowers set fruit shows that this cultivar can be highly self-compatible, at least under greenhouse conditions. In general, however, the experiment indicated a beneficial effect of cross-pollination since all three cultivars gave increased fruit sets when caged with another cultivar. The low percentages of set resulting from pairing Manzanillo and Mission supports data

presented in table 16 indicating that these two cultivars may show some cross-incompatibility.

### 1953 experiments

**Corning, California.** On May 1, 1953, branches were selected for bagging on 19 mature trees in a 10-acre solid block Sevillano orchard near Corning. The only possibility of cross-pollination was from a block of Manzanillo trees approximately 1/4-mile east and a block of Mission trees approximately 1 mile south. To help overcome the variation

TABLE 20  
EFFECT OF SELF-POLLINATION VERSUS CROSS-POLLINATION ON FRUIT SET OF  
OLIVE TREES IN THE GREENHOUSE AT DAVIS, 1952

Treatment	Cultivar	Number of trees	Number of inflores- cences	Number of flowers	Number of perfect flowers	Number of fruits set per 100 perfect flowers
Self-pollination (trees of one culti- var caged with nylon cloth to prevent cross-pollination).	Barouni	3	795	9,596	319	0.94
	Manzanillo	17	163	2,187	33	54.54
	Mission	3	993	12,137	1,787	2.29
Cross-pollination (trees of two culti- vars caged together to provide cross-pollination).	Barouni and Manzanillo	1	345	4,461	147	25.85
		4	86	1,558	27	81.48
	Barouni and Mission	1	143	1,583	142	37.32
		2	299	4,755	600	24.50
	Manzanillo and Mission	4	59	853	36	2.78
		2	240	2,332	625	0.32

in flowering habit among branches and sections of the same tree, groups of three similar branches on each tree were selected for study. There were 43 of these three-branch groups.

After counts of unopened flowers were made, two branches were bagged with 2-x 4-foot bags of double-thickness nylon cloth. The third branch was left as a naturally pollinated control. During the bloom period, May 15 through 21, one of the bagged branches in each of the 32 pairs was cross-pollinated by puffing either Mission or Manzanillo pollen into the bags with an aspirator (fig. 11). One of each of the remaining 11 pairs of bagged branches was artificially self-pollinated by puffing in Sevillano pollen gathered from trees and branches outside the bags. Each artificially pollinated branch received a capsule of pollen every 3 days until a total of three capsules had been puffed into each bag. The remaining bagged branch in each of the 43 pairs was left as a control to determine fruit set as effected by self-pollination. The bags were removed June 9 and the number of perfect flowers counted. Counts of normal and shotberry fruits were made on July 15. On October 15, fruits from the experimental branches were harvested and used for measurements to obtain further evidence on the possible role of xenia in olive fruit development. Table 21 summarizes the results.

The importance of cross-pollination for Sevillano is demonstrated by the significantly higher fruit sets on branches bagged and cross-pollinated, or subject to natural pollination, over those bagged only or bagged and self-pollinated by puffing in Sevillano pollen collected outside the bags. The differences in the amount of shotberries produced under the different

treatments were not significant. This does not agree with the 1952 data obtained at the Wolfskill Experimental Orchards at Winters, which showed that cross-pollination decreased production of shotberries while increasing the set of normal fruit.

Fruit measurements indicated that xenia has little or no influence on olive fruit development. There were no significant differences in the size of Sevillano fruits or pits produced under the different pollination treatments (table 21). Again, there was no apparent correlation between fruit set and fruit size. Evidently, within the range of fruit sets obtained (0.90 to 10.47 per cent), the highest fruit sets were not heavy enough to limit fruit growth under the conditions of this experiment.

**Winters, California.** An experiment similar to that described for Sevillano at Corning was set up for the Manzanillo cultivar at the Wolfskill Experimental Orchard, Winters. There were eight sets of three similar branches placed on large Manzanillo trees in an orchard consisting of several interplanted olive cultivars.

In each set, two of the three experimental branches were enclosed in large double-thickness nylon bags before the flowers opened. The third, unbagged branch was a naturally pollinated control. Table 22 lists the pollination treatments. Cross- and self-pollination was accomplished by using an aspirator to insert collected pollen.

Self-pollination by bagging only significantly reduced the set of normal fruits. Natural cross-pollination or pollination with Sevillano pollen gave the highest fruit sets by far. Setting of shotberry fruits followed a similar pattern but at a considerably lower level. Hence, cross-pollination failed to decrease the production of shotberries

# EFFECT OF DIFFERENT POLLINATION TREATMENTS ON SET OF NORMAL AND SHOTBERRY FRUITS AND ON SIZE OF NORMAL FRUITS AND PITS OF SEVILLANO (CORNING, 1953)

Pollination treatment of Sevillano flowers*	Number of perfect flowers	Mean number of normal fruits per 100 perfect flowers	Mean size of fruits and pits at harvest, October 15, 1953 (shotberries not included) <sup>§</sup>			
			Fruit length (mm)	Fruit width (mm)	Pit length (mm)	Pit width (mm)
Bagged control (self-pollinated) . . . . .	6,303	0.90	33.0a	24.9a	24.2a	11.2a
Bagged and self-pollinated with Sevillano pollen collected outside bag . . . . .	1,736	0.99	33.6a	24.8a	24.4a	11.0a
Bagged and cross-pollinated with Ascolano pollen . . . . .	1,260	7.21†‡	33.1a	24.3a	23.6a	11.1a
Bagged and cross-pollinated with Manzanillo pollen . . . . .	1,488	7.08†‡	34.8a	25.6a	25.1a	11.6a
Bagged and cross-pollinated with Mission pollen . . . . .	1,022	6.54§	34.7a	25.3a	25.0a	11.6a
Open or natural pollination (block of Manzanillo trees to the east) . . . . .	4,006	10.47†	34.0a	25.3a	24.4a	11.3a

\* Cross- and self-pollination (with the exception of the bagged control) accomplished by puffing pollen into bags with an atomizer.

† Significantly higher at the 1 per cent level than corresponding value for bagged control (self-pollination).

‡ Significantly higher at the 5 per cent level than corresponding value for self-pollination by puffing in 'Sevillano' pollen collected outside the bag.

§ Significantly higher at the 5 per cent level than corresponding value for self-pollination by puffing in 'Sevillano' pollen collected outside the bag.

¶ Mean values for fruit and pit size in the same column followed by the same letter are not significantly different at the 5 per cent level.

TABLE 22

# EFFECT OF DIFFERENT POLLINATION TREATMENTS ON SET OF NORMAL AND SHOTBERRY FRUITS AND ON SIZE OF NORMAL FRUITS AND PITS OF MANZANILLO (WINTERS, 1953)

Pollination treatment of Manzanillo flowers*	Number of perfect flowers	Mean number of normal fruits per 100 perfect flowers	Mean number of shotberry fruits per 100 perfect flowers	Mean size of fruits and pits at harvest, October 26, 1953 (shotberries not included) <sup>†</sup>			
				Fruit length (mm)	Fruit width (mm)	Pit length (mm)	Pit width (mm)
Bagged control (self-pollinated) . . . . .	4,162	0.88	0.12	23.3a	19.3a	13.9a	7.8b
Bagged and self-pollinated with Manzanillo pollen collected outside bag . . . . .	1,562	4.71†	1.06§	23.1a	19.4a	13.8a	8.0ab
Bagged and cross-pollinated with Mission pollen . . . . .	1,172	5.05†	0.72	23.7a	20.0a	14.1a	8.1a
Bagged and cross-pollinated with Sevillano pollen . . . . .	1,594	35.56††	2.49††	23.3a	19.2a	13.7a	7.5c
Open or natural pollination (cultivars interplanted) . . . . .	3,180	34.98††	2.07††	23.8a	20.0a	13.8a	8.1a

\* Cross- and self-pollination (with the exception of the bagged control) accomplished by puffing pollen into bags with an atomizer.

† Significantly higher at the 1 per cent level than corresponding value for bagged control (self-pollination).

‡ Significantly higher at the 1 per cent level than corresponding value for self-pollination by puffing in 'Manzanillo' pollen collected outside the bag.

§ Significantly higher at the 5 per cent level than corresponding value for self-pollination by puffing in 'Manzanillo' pollen collected outside the bag.

¶ Mean values for fruit and pit size in the same column followed by the same letter are not significantly different at the 5 per cent level.

although it did increase the set of normal Manzanillo fruits. This is similar to the situation with the caged trees of this and other cultivars in the same orchard in 1952 (table 14).

Fruit measurements (table 22) showed no evidence of xenia in the development of Manzanillo olives, thus corroborating the fruit-size data for this and other cultivars (tables 13, 18, 21). There were no significant differences in fruit size or pit length under different pollination treatments; differences in pit width were not correlated with self- or cross-pollination (table 22). The differences in fruit set apparently were not great enough to give significant differences in fruit size. This is surprising in view of the greater range of fruit sets (0.88 to 35.56 per cent) than was obtained previously (tables 13, 16, 21).

### 1957 and 1958 experiments

Year-to-year variations in amount of fruit set resulting from self-pollination indicated that weather conditions during the bloom and fruit-setting period could have significant influence on the degree of self-compatibility and self-fruitfulness among olive cultivars. To gain information regarding the influence of warm versus cool temperature conditions on pollen tube growth, fertilization, and fruit set following self- or cross-pollination, a number of 3-year-old Sevillano, Manzanillo, and Ascolano trees growing in 3-gallon containers were placed in two separate greenhouses on March 21, 1957. The trees ranged from 3 to 4 feet high. Such trees will flower profusely and set fruit under greenhouse conditions if their chilling requirements have been met by exposing them to outdoor temperatures during the winter. Four nylon-covered frames similar to those shown in figure 15 were constructed on a large bench in each greenhouse.

On April 17 groups of three uniform trees of each cultivar (as determined by numbers of developing inflorescences) were selected for study. For self-pollination experiments, trees of a single cultivar were isolated in individual compartments. For cross-pollination studies, trees of different cultivars were put in the same compartments.

One greenhouse, the so-called cool house, was not heated at night and the temperature usually dropped to between 50° and 55° F (10° and 12.8° C) between 4 and 6 A.M. Ventilators were kept open during the day to keep the temperature from rising above about 72° F (22.2° C) during the warmest hours. During a few days, however, the temperature in the cool greenhouse rose above 80° F (26.7° C). The thermostat in the warm greenhouse was set so that the night temperature did not drop below 62° F (16.7° C). The maximum temperature in the warm greenhouse was usually about 88° F (31.1° C) and ventilators were not opened unless the temperature rose above 90° F (32.2° C). Mean temperatures during the flowering and fruit setting period in the cool greenhouse averaged about 10° F (5.5° C) below those recorded in the warm greenhouse. Temperature records were obtained from thermographs operated in the nylon-covered compartments in the greenhouse during the time the experiments were conducted.

The flowers on the Manzanillo trees in the warm greenhouse started opening April 22. They were judged to be in full bloom on April 27, and in the stage of last effective bloom for pollination on May 1. Dates of first bloom, full bloom, and last bloom for Ascolano were April 23, April 29, and May 3; for Sevillano they were April 24, April 29, and May 3.

In the cool greenhouse, dates of first

bloom, full bloom, and last bloom for the three cultivars were: April 30, May 5, and May 11 for Manzanillo; May 3, May 8, and May 17 for Ascolano; and May 6, May 12, and May 17 for Sevillano. Hence, in 1957 the temperatures in the cool greenhouse were enough lower than those in the warm greenhouse to delay full bloom 8 days in Manzanillo, 9 days in Ascolano, and 13 days in Sevillano.

Essentially the same experiment as described for 1957 was repeated in 1958 with winter-chilled trees brought into the greenhouse on March 6, 1958. In 1958, the 10° F (5.5° C) temperature differential between the warm and cool greenhouses, as maintained in 1957, was not as easily obtained due to weather conditions. In 1958, the maximum temperatures were often the same in both houses but the minimum temperatures were consistently 5° to 8° F (3° to 4.5° C) higher in the warm than in the cool greenhouse. Based on plant response as indicated by time of bloom, however, the difference in the average temperatures maintained in the warm and cool greenhouse was greater in 1958 than in 1957. The 1958 dates of first bloom, full bloom and last bloom for trees in the warm greenhouse were April 11, April 14, and April 17 for Manzanillo; April 13, April 16, and April 22 for Ascolano; and April 13, April 17, and April 20 for Sevillano. In the cool greenhouse the corresponding dates of first, full, and last bloom were April 28, May 1, and May 7 for Manzanillo; April 29, May 4, and May 13 for Ascolano; and April 30, May 7, and May 11 for Sevillano. The difference in temperature between the warm and cool greenhouses, therefore, accounted for delaying full bloom 17 days in Manzanillo, 18 days in Ascolano, and 20 days in Sevillano.

In 1957 and 1958, approximately

the same procedures for study of pollen tube growth were followed. Before flower opening, tags were placed on inflorescence branches containing from one to five flowers, and the branches were then examined twice daily for open flowers. As the perfect flowers opened, their anthers were removed with small scissors before dehiscence. Immediately thereafter they were either cross-pollinated or self-pollinated by hand with a camel-hair brush and pollination time and date were recorded on the tag. Samples consisting of 10 hand-pollinated flowers were collected at 1- or 2-day intervals for 14 or more days after pollination from experimental trees of each cultivar in both greenhouses. Individual hand-pollinated flowers were clipped from the branch of the inflorescence and dropped into a vial of fixative solution, and the samples were taken to the laboratory for embedding in paraffin. The pistils were sectioned and stained to show the pollen tubes and were studied under the microscope. A record was made of the longest pollen tube in each pistil, and whether it had stopped growth in the stigma, the style, or the ovary, or had reached the embryo sac. Tables 23 and 24 show the effects of cross- versus self-pollination and of temperature on pollen tube growth of these three cultivars.

In self-pollinated Ascolano in 1957, some pollen tubes reached embryo sacs in the relatively brief period of 3 days after pollination in the warmest greenhouse (57W), but in the warm greenhouse in 1958, 8 days elapsed after pollination before any tubes were seen in embryo sacs (table 23). No pollen tubes reached embryo sacs in the cool greenhouse in either year, however. Although rapid pollen-tube growth occurred in the warmest house, and pollen tubes were found in 40 per cent of the embryo sacs after self-pollination

TABLE 23

INFLUENCE OF TEMPERATURE ON NUMBERS OF DAYS REQUIRED FOR POLLEN TUBES (A) TO GROW THROUGH THE STIGMA AND (B) TO REACH EMBRYO SACS IN SELF- AND CROSS-POLLINATIONS OF THREE OLIVE CULTIVARS (DAVIS, 1957, 1958)

Cultivar and pollination	Year and greenhouse (W=warm, C=cool)	Number of days after pollination		Temperature (° F) during the 10 days after pollination	
		A	B	Temperature range	Frequency means
Ascolano × self . . . . .	57W	2	3	62-92	74.8
Ascolano × self . . . . .	58W	5	8	56-86	69.8
Ascolano × self . . . . .	58C	9	—	51-86	68.1
Ascolano × self . . . . .	57C	12	—	56-91	66.4
Manzanillo × self . . . . .	57W	—	—	62-92	74.8
Manzanillo × self . . . . .	58W	9	15*	59-86	70.6
Manzanillo × self . . . . .	58C	—	—	51-85	67.4
Manzanillo × self . . . . .	57C	—	—	56-91	67.1
Sevillano × self . . . . .	58W	3	6	59-86	70.5
Sevillano × self . . . . .	58C	4	7*	51-86	67.2
Ascolano × Manzanillo . . . . .	57W	2	3	62-92	74.8
Ascolano × Manzanillo . . . . .	58W	4	8*	59-86	70.7
Ascolano × Manzanillo . . . . .	58C	6	12*	51-86	68.1
Ascolano × Manzanillo . . . . .	57C	7	14*	56-91	66.4
Ascolano × Sevillano . . . . .	58W	1	2	59-86	70.5
Ascolano × Sevillano . . . . .	58C	2	2	51-86	68.1
Manzanillo × Ascolano . . . . .	57W	2	3	62-92	74.8
Manzanillo × Ascolano . . . . .	57C	11	13*	56-91	67.1
Manzanillo × Sevillano . . . . .	58W	1	2	56-86	69.8
Manzanillo × Sevillano . . . . .	58C	2	2	51-86	67.2
Sevillano × Manzanillo . . . . .	58W	1	3	59-86	70.5
Sevillano × Manzanillo . . . . .	58C	3	7	51-86	67.2

\*Presence of two or more endosperm nuclei in the sacs showed that tube penetration had occurred earlier than the day indicated.

TABLE 24

POLLEN-TUBE GROWTH IN SELF- AND CROSS-POLLINATIONS OF THREE OLIVE CULTIVARS (DAVIS, 1957, 1958)

Cultivar and pollination	Year and greenhouse (W=warm, C=cool)	Total pistils*	Percentages of pistils with pollen tubes in or on				
			Stigma	Style	Ovary wall	Locule or ovule	Embryo sac
Ascolano × self . . . . .	57W	50	40	12	8	0	40
Ascolano × self . . . . .	58W	68	73	0	7	2	18
Ascolano × self . . . . .	58C	36	83	3	8	6	0
Ascolano × self . . . . .	57C	23	74	13	13	0	0
Manzanillo × self . . . . .	58W	26	69	0	16	0	15
Sevillano × self . . . . .	58W	78	50	4	29	12	5
Sevillano × self . . . . .	58C	69	70	1	19	9	1
Ascolano × Manzanillo . . . . .	57W	49	10	4	10	15	61
Ascolano × Manzanillo . . . . .	58W	56	71	2	11	7	9
Ascolano × Manzanillo . . . . .	58C	47	79	2	13	0	6
Ascolano × Manzanillo . . . . .	57C	58	76	0	12	3	9
Ascolano × Sevillano . . . . .	58W	40	12	2	26	26	34
Ascolano × Sevillano . . . . .	58C	38	5	0	8	11	76
Manzanillo × Ascolano . . . . .	57W	50	10	6	8	8	68
Manzanillo × Ascolano . . . . .	57C	36	50	12	0	0	38
Manzanillo × Sevillano . . . . .	58W	53	17	8	17	41	17
Manzanillo × Sevillano . . . . .	58C	34	6	8	12	12	62
Sevillano × Manzanillo . . . . .	58W	76	4	15	47	24	10
Sevillano × Manzanillo . . . . .	58C	47	64	15	17	2	2

\*Includes only pistils collected on or after the date when pollen tubes were first found below the stigma.

TABLE 25  
FRUIT SETS OBTAINED IN SELF-POLLINATIONS AND CROSS-POLLINATIONS OF THREE OLIVE CULTIVARS  
UNDER DIFFERENT TEMPERATURE CONDITIONS (DAVIS, 1957, 1958)

Cultivar	Treatment		Number of inflorescences		Number of perfect flowers		Number of normal fruits per 100 perfect flowers		Number of shoddy fruits per 100 perfect flowers	
	Pollination	Greenhouse condition	1957		1958		1957		1958	
			1957	1958	1957	1958	1957	1958	1957	1958
Ascolano	Self-pollination	Warm	863	453	2,725	2,615	2.09*	2.79*	0.22	0.42
Ascolano	Self-pollination	Cool	388	674	1,956	5,115	0.26	1.37	0.20	0.33
Ascolano	Cross-pollination	Warm	922	556	1,526	2,292	9.96**	6.98**	0.13	0.83*
Ascolano	Cross-pollination	Cool	341	891	2,408	6,275	3.32†	2.18†	0.75*	0.38
Manzanillo	Self-pollination	Warm	43	1,097	185	1,631	0.00	0.61	0.00	0.06
Manzanillo	Self-pollination	Cool	61	431	494	1,847	0.00	1.79*	0.00	0.16
Manzanillo	Cross-pollination	Warm	106	628	261	515	15.71**	6.80†	0.38	0.97†
Manzanillo	Cross-pollination	Cool	147	986	769	1,793	4.55†	4.80†	0.39	0.95†
Sevillano	Self-pollination	Warm	31	655	14	1,979	7.14	5.10*	0.00	0.35
Sevillano	Self-pollination	Cool	17	1,787	88	1,597	4.54	1.69	2.27	6.45**
Sevillano	Cross-pollination	Warm	52	368	133	932	7.52	7.62**	8.27	2.36**
Sevillano	Cross-pollination	Cool	4	177	22	1,315	18.18‡	2.21	0.00	0.53

\*Significantly greater at the 1 per cent level than the corresponding value for the same cultivar under the opposite greenhouse condition.

†Significantly greater at the 1 per cent level than the corresponding value for the same cultivar under the opposite pollination treatment.

‡Significantly greater at the 5 per cent level than the corresponding value for the same cultivar under the opposite pollination treatment.

(table 24), the effects of cross-pollination were still superior. Manzanillo pollen tubes grew no more rapidly than did those of Ascolano in Ascolano pistils in the warmest house but entered a higher percentage of embryo sacs. Also, in cool greenhouses in both years some embryo sacs were entered by Manzanillo pollen tubes. Sevillano pollen tubes grew even more rapidly in Ascolano pistils in both warm and cool greenhouses, and reached 76 per cent of the embryo sacs in the cool house but only 34 per cent in the warm house. Fruit-set data (table 25) also illustrate the beneficial effects of cross-pollination for Ascolano.

In self-pollinated Manzanillo, no pollen tubes grew through the stigmas in the warmest greenhouse (table 23), although pollen germination was excellent (table 24). Moreover, none grew through the stigmas in either of the cool greenhouses. Only in the moderately warm greenhouses did pollen tubes reach embryo sacs, but so much time was required that probably some embryo sacs degenerated, for pollen tubes were seen in only 15 per cent of the pistils. These failures in self-pollination are reflected in the fruit-set data (table 25). In the cross-pollinations Manzanillo x Ascolano and its reciprocal, pollen-tube growth was greatly improved, particularly in the warmest greenhouse (table 23) and some tubes reached sacs even in the coldest greenhouse. Table 25 shows a high percentage of normal fruit resulting from cross-pollination in the warmest greenhouse and, as expected, progressively lower percentages as greenhouse temperatures decreased. These results show that self-pollinated Manzanillo is extremely sensitive to high temperature, which indicates self-incompatibility. The highest temperatures seemingly induced strong incompatibility reactions that inhibited pol-

len-tube growth through the stigmas, while temperatures in the cool greenhouses also prevented adequate tube growth.

Pollen tubes in self-pollinated Sevillano required 6 days to reach embryo sacs in both warm and cool greenhouses in 1958 (table 23). In only 5 per cent of the pistils in the warm house and 1 per cent in the cool house did pollen tubes reach embryo sacs (table 24); fruit-set data for self-pollinated Sevillano conform with these figures (table 25). Pollination of Sevillano pistils with Manzanillo pollen doubled the 5 and 1 per cent figures obtained with Sevillano self-pollinated (table 24). In the two crosses with Sevillano as the pollen parent, however, the percentages of pollen tubes reaching sacs were considerably increased, partly at least because of the rapid growth of Sevillano pollen tubes in either Manzanillo or Ascolano pistils even in the cool greenhouse in 1958 (table 23). Fruit-set in that greenhouse was relatively high (table 25), which suggests that Sevillano would be an excellent pollenizer in cool weather as well as a moderately effective one in hot weather.

The presence of a pollen tube in an embryo sac did not always ensure fertilization. If pollen tube growth was too slow, the sac began to degenerate before the tube reached it. However, the chances of fertilization were greater in cross- than in self-pollinations, as indicated by the higher percentages of pistils in which a pollen tube reached an embryo sac.

In most of the pollinations, warm temperatures were favorable for pollen-tube growth. However, in the cross-pollinations in which Sevillano pollen was used, cool conditions were equally favorable. Higher temperatures increased the incompatibility reactions, and pollen tubes more fre-

quently became blocked somewhere between stigmas and embryo sacs. Of the three cultivars tested, Manzanillo appeared to be the most self-incompatible and Ascolano the least so.

Pollination for fruit-set data in the 1957 and 1958 warm and cool greenhouse experiments was enhanced by operating electric fans in all compartments for two 20-minute periods a day for several days during full bloom. In the cross-pollination compartments, the pollen parent concerned in setting of any fruit was unknown. The purpose had been to compare fruit-set from self-pollination versus cross-pollination, irrespective of pollen donors. Soon after petal fall the perfect flowers on each tree were counted—trees were taken outdoors 1 or 2 weeks after that. Each year fruits were counted early in June, and again near harvest time. Table 25 shows the results of these counts.

In 1957 and 1958 larger sets of normal fruits were obtained on the trees exposed to cross-pollination than on those limited to self-pollination. Also, both self- and cross-pollinated trees in the warm greenhouse generally gave heavier sets of normal fruit than corresponding trees in the cool greenhouse. With Sevillano the differences in normal fruit-set between self-pollinated (7.14 per cent) and cross-pollinated trees (7.52 per cent) in the warm greenhouse in 1957 and in the cool greenhouse in 1958 (1.69 and 2.21 per cent) were not significant. Few perfect flowers were formed on the Sevillano trees in 1957, so data about them may be questionable. In 1958, set of normal fruit on both self- and cross-pollinated Sevillano trees in the cool greenhouse was relatively low.

The fruit-set data in table 25 generally augmented the data in table 24 which are concerned with pollen-tube

growth into embryo sacs, thus indicating that larger samples of self-pollinated pistils from Ascolano trees under cool greenhouse conditions in both 1957 and 1958, and from Manzanillo trees in the cool greenhouse in 1958, might have included some with tubes in sacs. The fruit-set data also confirmed the evidence in self-pollinated Manzanillo that, in the warmest and coldest greenhouses, pollen tubes failed to reach sacs.

For many pollinations, the percentages of pistils with tubes in embryo sacs were much higher than corresponding percentages of fruit-set. The differences between those percentages probably represent primarily the incidence of disorders of fertilization or post-fertilization phases. In self-pollinated Manzanillo, in which tube growth was excessively slow, degeneration of embryo sacs by the time tubes reached some of them may have accounted in part for the difference between percentages of tubes in sacs and of fruit-set. The differences were particularly large in self- or cross-pollinated pistils of Ascolano and Manzanillo wherever conditions had been most favorable to tube growth into sacs. By contrast, in self-pollinated Sevillano and in Sevillano x Manzanillo, the differences in percentages of tubes in sacs and of fruit-set were so small that they could scarcely be considered significant.

Ascolano and Manzanillo trees produced relatively low percentages of shotberry fruits under all treatments in 1957 and 1958 (table 25). In 1958, self-pollinated Sevillano trees in the cool greenhouse produced significantly more shotberries than did comparable cross-pollinated trees. With all cultivars, however, there was no consistent relationship between treatments or set of normal fruits and production of shotberry fruits.

## DISCUSSION AND CONCLUSION

In most years, there is sufficient overlap in bloom to permit adequate cross-pollination among the various olive cultivars grown commercially in California. The only exception to this may be the combination of Ascolano and Barouni because in one year at least (1954) full bloom in Ascolano occurred 7 days later than did bloom in Barouni. Blooming dates for olives in California's Central Valley can vary widely from year to year depending upon the spring temperature; cool, wet springs (e.g., in 1967) can delay full bloom until early June, and hot weather in April and May can cause rapid flower development, with full bloom in early May.

For pollination experiments with olives, or to obtain large supplies of pollen for artificial pollination of olive orchards, collection of pollen in quantities is considerably more difficult than for other fruit species. Anthers from olive flowers cut off the tree do not dehisce and shed pollen readily. An efficient method of collecting olive pollen is to place large paper bags over branches shortly before the flowers open and then, after 7 to 10 days, remove the bags and empty their contents onto large sheets of glass from which they can be scraped onto cheesecloth for filtering out petals and other flower parts.

Olive pollen shows good viability, with germination percentages ranging from 20 to 70 per cent. There seem to be no consistent differences in pollen viability among California olive cultivars. Olive pollen maintains viability at low temperatures and has been held for  $3\frac{1}{2}$  years in sealed containers at  $0^{\circ}$  F ( $-18^{\circ}$  C) with germination percentage loss, for an average of 5 cultivars, from 47.6 down to 25.5 per cent. Pollen collected from bagged branches

or from inside nylon-covered trees usually has as much viability as does pollen taken from exposed branches. In these tests, temperature and humidity differences developing as a result of branch or tree enclosures did not seem to have any deleterious effects on pollen viability.

If dependence is to be made on cross-pollination in olives, and with the wind being the primary moving agent for the pollen, it is important to know what distance olive pollen is likely to be moved. According to the results of these tests, pollenizer trees should be planted in an orchard so that the receptive trees are no farther than 200 feet away. If there are pronounced prevailing winds in the area this should be taken into consideration in laying out the orchard. While olive pollen can be found several miles on the leeward side of an olive district having a consistent wind pattern, this is too great a distance for dependable cross-pollination effects.

Honeybees usually collect pollen in olive trees during bloom, and it is possible that their activity enhances cross-pollination if trees of two or more cultivars are planted in close proximity. It is obvious from the high fruit-sets obtained when branches were bagged with bee-impervious netting (table 9) that bee activity is not a requirement for fruit setting in olives. On the other hand, the significantly higher fruit-sets obtained (table 10) when container-grown mixed cultivar trees were set as close as 15 feet to a row of honeybee hives, with the flowers being heavily worked by bees, indicate some beneficial influence due to bee activity.

Experiments using seven olive cultivars were conducted in 1950, 1951, 1952, 1953, 1957, and 1958 comparing

fruit-set under situations permitting only self-pollination with those providing cross-pollination in addition to self-pollination. Uncontrolled cross-pollination was prevented either by bagging branches with pollen-proof cloth or paper bags, or by enclosing whole trees or portions of trees in pollen-proof cloth-covered frames before the flowers opened. Orchard trees in several locations, as well as container-grown trees placed in the greenhouse, were used for the experiments reported here.

In noting the variable results shown in tables 10 through 20, it is apparent that a considerable number of trials must be carried out to develop meaningful and correct conclusions as to possible benefits from cross-pollination in enhancing fruit-set in olives. A single experiment under one set of environmental conditions would be of little value in developing general conclusions.

It is apparent that comparatively high fruit-sets can take place in olives under certain conditions without cross-pollination (tables 12, 13). The problem then becomes to what extent, if any, cross-pollination increases fruit-set. In the tests reported here this did occur in most of the experiments, and considerably higher fruit-sets often occurred when cross-pollination was available in comparison with self-pollination alone (tables 11, 14, 16, 19, 20, 21, 22, 25).

Temperature strongly influences plant reactions and is a dominant factor that can vary considerably from year to year and place to place during olive pollination, fertilization, and fruit-setting periods. The 1957 and 1958 experiments (p. 38), in which groups of container-grown trees placed in separate greenhouses were allowed to go through these periods at an approximate 10° F (5.5° C) temperature

differential, give some information on how different temperature levels may influence ultimate fruit-setting under self- versus cross-pollination conditions.

The 10° F temperature differential had a definite influence on pollen-tube development in the pistils; growth was generally faster under the higher as compared to the lower temperatures. Responses of different self- and cross-pollination combinations to high versus low temperatures varied (tables 23, 24). Generally, pollen tubes grew faster through the stigma, style, and into the embryo sac with cross-pollination than they did with self-pollination in either of the temperature situations. Hence, the chances of fertilization and fruit-set are much greater following cross-pollination compared to self-pollination because more pollen tubes can reach the embryo sacs before the sacs degenerate.

A significant finding in these studies is that Manzanillo pollen-tube growth in Manzanillo pistils (self-pollinated Manzanillo) is extremely sensitive to high temperatures, thus indicating self-incompatibility. This could explain the poor fruit-set in this cultivar often occurring with exceptionally hot weather at bloom. But these studies also disclosed that, in regard to pollen-tube growth, genetic incompatibility within a cultivar (and to some extent between cultivars) may be more important than are temperature effects. If certain identical genes are present in both a pistil and a particular pollen grain, tube growth will be blocked at some point by inhibiting substances that are rapidly formed by the pistil in reaction to the pollen grain or tube. The incompatibility reaction is so strong in these cultivars, either self- or cross-pollinated, that it usually prevents all but one pollen tube from growing below the stigma. The incom-

patibility effect was particularly noticeable in self-pollinated cultivars. The percentages of pistils in which a pollen tube grew beyond the stigma were low in self-pollinations as compared with cross-pollinations, and the percentages of pistils in which a pollen tube reached an embryo sac were even lower.

There are indications from some of the cross-pollination combinations included in these tests that Mission and Manzanillo show cross-incompatibility. As shown in table 16, Manzanillo pollinated by Mission gave the lowest fruit-set count among the 5 pollinating cultivars used. Similarly, Mission pollinated by Manzanillo had the lowest fruit-set counts among the 5 pollenizers used. In addition, trees of the Manzanillo x Mission combination used in the experiments summarized in table 20 showed far lower fruit-sets than did trees of the Barouni x Manzanillo and Barouni x Mission combinations.

An important problem in California olive production, particularly with Sevillano, is the development of the undersized, misshapen fruits called shotberries (figs. 13 and 14). The incidence of such fruits in an orchard varies widely from year to year, indicating that their development is caused by some variable factor or factors. The presence of shotberries must result from parthenocarp or some abnormality in the seed-formation process, because such fruits almost always have no seed within the endocarp (tables 15, 17). Attempts to associate shotberry production with pollination situations are summarized by data presented in tables 14, 15, 16, 17, 21, 22, and 25. As shown in table 14, enclosing trees in pollen-proof nylon cages to prevent cross-pollination greatly increased shotberry production as compared to trees subjected to cross-

pollination; this was particularly true for both Manzanillo and Mission.

Manzanillo, when self-pollinated by bagging only or pollinated with Manzanillo pollen (table 16), produced, respectively, 11.3 and 31.8 shotberry fruits per 100 perfect flowers. When Ascolano, Barouni, Mission, or Sevillano was used as the pollen source, shotberry development per 100 perfect flowers was 0.21, 0.00, 0.00, and 0.00, respectively. However, in other tests there was no relationship between the type of pollination and the incidence of shotberries.

If most shotberry fruits are the result of parthenocarpic fruit-set, then tree vigor may have a greater influence on production of these undesirable fruits than either self- or cross-pollination, with greater vigor leading to an increased incidence of shotberry fruits.

To ensure maximum fruit production from olive orchards every year it would be advisable to arrange for cross-pollination. Although not all the individual experiments reported here showed increased fruit-set with cross-pollination, most did show such an increase.

The study of wind dissemination of olive pollen (table 7, figure 9) indicates that olive cultivars should be planted within 100 feet of each other for good cross-pollination. With equal numbers of two cultivars it is advisable, for convenience in harvesting, to plant four rows of one cultivar, then four of another, then repeat. Where disproportionate numbers are desired, plant one or two rows of a cultivar, then four of another, etc. To grow one principal cultivar with the pollenizing cultivar kept to a minimum, one tree to eight, planted as every third tree in every third row should give satisfactory results. These recommendations are comparable to those

made by workers in Italy (Morettini, 1941) and Argentina (Molinari and Nicolea, 1947).

Of the olive cultivars grown commercially in California, two combinations, Manzanillo x Mission and Sevillano x Barouni, showed evidence of inter-incompatibility (table 16). If either of these combinations is the only one in an orchard, the introduction of a different cultivar as a pollinizer may improve fruit-set and yields.

Measurements of fruits (excluding shotberry fruits) during 3 years revealed no evidence of xenia in olive

fruit development (tables 13, 18, 21, 22) among the olive cultivars. Size of fruits and pits resulting from self-pollination alone were not consistently different from those resulting from self- plus cross-pollination. Also, there were no consistent differences in fruit size that could be attributed to the use of one pollinizer cultivar versus another. For each cultivar, under the range of fruit-sets (percentages of perfect flowers that produced fruit) obtained in these experiments, size of fruits was remarkably uniform regardless of pollination treatment.

## ACKNOWLEDGMENTS

The assistance of Robert M. Hoffman, former Farm Advisor, Tehama County, in the experiments at Corning is gratefully acknowledged.

We also wish to extend appreciation to Karl W. Opitz, Extension Subtropical Horticulturist, for reviewing the manuscript.



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